

SYSTEMATICS OF *LEUCOPHYLLUM* AND *EREMOGETON* (SCROPHULARIACEAE)

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ABSTRACT

Leucophyllum and *Eremogeton* were placed in Leucophylleae series Pseudosolaneae by Benth and in Verbasceae by Wettstein at the base of Scrophulariaceae. The two genera have been considered somewhat anomalous in Scrophulariaceae because of their woody habits and other features. Recent comparisons have shown similarities with woody Myoporaceae but the woody habit of *Leucophyllum* appears to be derived; this and comparisons of ovary structure show relationships are clearly with Scrophulariaceae. Data from comparative anatomy and morphology of leaves, stems, flowers, and trichomes, from chromosome number, and from phytogeography suggest recognition of 12 species of *Leucophyllum* including *Faxonanthus* as a monotypic subgenus. The species range from Puebla north through arid portions of Mexico into southern Texas. *Leucophyllum langmaniae* and *L. ultramonticola* are described as new. *Eremogeton*, retained as a monotypic genus related to *Leucophyllum*, is endemic to Central America.

INTRODUCTION

Since its inception, *Leucophyllum* has been placed in Scrophulariaceae, however, its position within the family has varied. Benth (1846), in de Candolle's *Prodromus*, placed the genus in his suborder (subfamily) Antirrhinidae, tribe Gratioleae, subtribe Aptosimeae, next to the Old World genera *Aptosimum* Burchell, *Peliostomum* E. Mey., *Anticharis* Endl., and *Doratanthera* Benth. ex Endl. (= *Anticharis*).

Later, Benth (1876) in his *Genera Plantarum* treatment, placed *Leucophyllum* along with *Ghiesbrechtia* Gray (= *Eremogeton* Standl. & Williams) and *Heteranthia* Nees & Mart. (a monotypic Brazilian genus now placed in Solanaceae) in his series Pseudosolaneae (with alternate leaves, simple centripetal inflorescences, corolla with posterior lobes external in bud), tribe Leucophylleae (corolla tubes campanulate), at the base of the family next to the South African Aptosimeae (with *Aptosimum*, *Plisotomum*, and *Anticharis*) and the Old World Verbasceae (with *Verbascum* L., *Celsia* L., and *Stanrophragma* Fisch. & E. Mey.).

Wettstein (1891), in Engler and Prantl's *Natürlichen Pflanzenfamilien*, placed *Leucophyllum* and *Gbiesbrechtia* in the series Pseudosolanaceae, tribe Verbasceae (again next to Aptosimeae) and emphasized the multicellular, branched trichomes, mostly axillary flowers with actinomorphic or zygomorphic corollas with short, campanulate tubes and 5 stamens with anther thecae united at the tip or throughout. Within the tribe the New World genera were separated from the Old World *Verbascum*, *Celsia*, and *Staurophragma* on the basis of campanulate corolla tubes, anther sacs united at tips only, and solitary, axillary flowers.

Flyr (1970) suggested that *Leucophyllum* may best be placed in Myoporaceae. In an analysis of pollen, Niezgoda and Tomb (1975) showed that, unlike most Scrophulariaceae, *Leucophyllum*, *Faxonanthus* (here treated as a subgenus of *Leucophyllum*), and *Eremogeton* have distinctive, prolate or oblate—spheroidal, 3-colpate, diorate pollen, characterized by two elliptical apertures on each colpus, one at each side of the equator, a condition also found in the three genera of the Myoporaceae: *Bontia* L., *Eremophila* R.Br., *Myoporum* Soland. ex Forst.f. As noted by Niezgoda and Tomb (1975), however, the same pollen type is present in *Capraria* L. (Scrophulariaceae). Argue (1980) noted similar pollen in sections *Mimulus* and *Erythranthe* of *Mimulus* L., in several genera of the Gratiroleae (*Lancea* Hook.f. & Thoms., *Artanema* D. Don. and *Conobea* Aubl.), in *Penstemon* Mitch. of the tribe Cheloneae, and in *Celsia* of Verbasceae. On the basis of pollen data, Niezgoda and Tomb (1975) suggested the tribe Leucophylleae be transferred to the Myoporaceae as a subfamily. However the paper by Argue (1980) weakens their argument. Tomb (pers. comm. 1984) has recently found similar 3-colpate, diorate pollen in Bignoniaceae.

Karrfalt and Tomb (1983) suggested ontogenetic similarities between the epithelium-lined secretory cavities of *Bontia* (Myoporaceae) and the larger, non-lined air cavities in leaves of selected leucophyllums noting that scattered cells surrounding the air cavities in *Leucophyllum* have epithelial-like expansions. They also cited the occurrence of branched multicellular trichomes on vegetative buds on *Bontia*, the co-occurrence of isobilateral leaf structure in *Leucophyllum* and some species of *Eremophila* and *Myoporum*, and noted the similarity in habit between the shrubby, gray-leaved *Leucophyllum* and some *Eremophila*.

In spite of these and other similarities, there exist strong differences between *Leucophyllum* and Myoporaceae, particularly in gynoecial and fruit characters. As noted by Karrfalt and Tomb (1983), the 2-carpelled, 2-loculed, superior ovaries with axile placentas, many ovules, and septicial capsules that also open loculicidally at the tip that characterize *Leucophyllum* and *Eremogeton* are typical of Scrophulariaceae but unlike the conditions

found in Myoporaceae. To this we may add that the campylotropous ovules and seed structure of *Leucophyllum* and *Eremiogeton* are also identical to that of Scrophulariaceae.

While Myoporaceae also tend to have 2-carpelled ovaries with placenta oriented in a manner similar to that of Scrophulariaceae (i.e. with enlarged placenta intruding into the locules perpendicularly from the ovary septum) the placentae in Myoporaceae often extend all the way to the outer ovary wall forming false and incomplete septa that effectively divide each carpel into 2 locules. In some species placentae are not so well developed and carpels are unilocular. Ovaries of *Myoporum*, in contrast, typically are divided into 2–4 (up to 12 in *Myoporum sandwicense* A. Gray) (Webster 1951) uniovulate compartments and this has been interpreted as consisting of 2 carpels divided by supernumerary partitions (Cronquist 1981) or it could possibly be a multicarpellate ovary with up to 6 carpels. Ovules are few in number, typically 1–3 (very rarely 4) pair per carpel, and when consisting of 2 or more pair per carpel, the ovules are superimposed in the narrow locules bordering the intruded placentae. Unlike the Scrophulariaceae or Leucophylleae ovules are pendulous, anatropous with micropyles superior (Wettstein 1895; Chinnock pers. comm. 1984).

Differences also occur in stigma structure. In the Leucophylleae style tips are expanded, flattened, rounded to acute and stigmatic along the somewhat thickened distal margins. In Myoporaceae style tips are either capitate (*Myoporum*) or more often slender with stigmatic surfaces restricted to a notch at the slender tips, with this rarely expanded into a slightly bifid tip (Chinnock idem.).

Unlike the Scrophulariaceae and Leucophylleae mature fruit of Myoporaceae are indehiscent and can be dry or drupaceous. The endocarp of the fruit walls can be thickened and sclerified or thin and rather cartilaginous (Chinnock idem.). The exocarp can be dry and papery and separable from the endocarp by breakdown of the mesocarp. The mesocarp is often dry, pithy or firmly pithy. These dry fruit are indehiscent but there may be some disintegration of tissue near the top of the ovary and carpels may separate slightly (Chinnock idem.). In *Myoporum* and some species of *Eremophila* the mesocarp is thickened and fleshy and the fruit are considered drupaceous though there may be several seeds from more than one carpel inside the hardened endocarp (Chinnock idem.). As ovule number in Myoporaceae typically ranges from 1–3 pair per carpel, fruit have only 1–8(–12) seeds and these are much larger than in the Leucophylleae measuring 2–3.5 mm in length with testa surfaces smooth or faintly reticulate (Chinnock idem.). Unlike the Scrophulariaceae and Leucophylleae seeds have scanty or no endosperm.

While Myoporaceae appear to be uniformly woody, data presented here indicate that *Leucophyllum* may be secondarily woody, i.e., derived from herbaceous ancestors. Woody growth habits, of course, also occur in other tribes of the Scrophulariaceae.

Species of *Leucophyllum* are very similar vegetatively to some species of *Eremophila*. As they both occur in semiarid and arid habitats, this to some degree may be convergence. They both have dorsi-ventral to isobilateral leaves, and can be pubescent to densely canescent often with dendritically-branched hairs. In both, corollas can be weakly zygomorphic, though *Eremophila*, with 140 species (Chinnock idem.), exhibits considerably more diversity with corollas ranging from nearly actinomorphic to strongly zygomorphic, with some species having 4 posterior corolla lobes and solitary anterior lobes. The corolla and androecium of *Leucophyllum* strongly resemble those of some species of *Myoporum* (e.g. *M. laetum*) even down the surface texture of the corolla trichomes and in the arrangement of the anther sacs. However, many of these characteristics occur throughout both families. There, however, remain significant differences between the families in gynoecial features, and chromosome numbers etc.

While *Leucophyllum* and *Eremogeton* may constitute a somewhat discordant element within Scrophulariaceae, they are strongly discordant in Myoporaceae and their inclusion in that family would completely go against the few (mostly gynoecial) characters that distinguish Myoporaceae from Scrophulariaceae. On the other hand, there are so many characteristics in common between Myoporaceae and Scrophulariaceae that recognition of Myoporaceae as a distinct family could be questioned.

In the paragraphs below we present data on morphology, anatomy, and cytology of *Leucophyllum* and *Eremogeton* and wherever possible we comment on characteristics found in other Scrophulariaceae and/or Myoporaceae. The picture that emerges is that in many features *Leucophyllum* and *Eremogeton* are similar to both families and in other features (some critical) they are more similar to Scrophulariaceae. These data plus phytographic considerations, discussed below, support retention of *Leucophyllum* and *Eremogeton* in the tribe Leucophylleae, series Pseudosolaneae, at the base of the Scrophulariaceae along with other Old World tribes as initially suggested by Bentham (1876).

MORPHOLOGY AND ANATOMY

HABIT: *Leucophyllum* species are mostly small- to medium-sized, rounded shrubs 0.5 – 2.5 m tall with divaricately branching stems. Branching may be ascending or divergent. In some species, dead branches persist and give the plants a thorny aspect. The habit of *L. pringlei* differs from others in its

basal woody burl from which arise several, slender, erect stems that branch only in the distal portion. *Eremogeton*, which neither of us has seen, is apparently a taller, branched shrub to small tree 1.5–8 m high (*fide* labels). YOUNG STEMS: Young stems of *Leucophyllum* are terete and vestitured. The nodes develop distinct, persistent protuberances, and long-shoot leaves abscise just above the swollen bases. Anatomically, young stem pith initially consists of large parenchyma cells that develop into lignified brachysclereids within the first year. Vascular tissue develops in a continuous ring, i.e., not broken by medullary rays (see xylem description below). A continuous ring of primary phloem fibers to 0.06 mm thick in *Leucophyllum*, to 0.2 mm thick in *Eremogeton*, occur outside the non-lignified phloem. This cylinder of fibers is broken apart as stems increase in diameter. In some species the areas between the primary phloem fibers develop brachysclereids. The cortex is parenchymatous, the outer portion consisting of chlorenchyma and later storing starch. A phellogen develops in the outermost cortex layer immediately beneath the epidermis. Periderm (phellem) cells do not collapse radially, and the cork is often soft and thickened. In several species (e.g., *L. revolutum*, *L. pruinsum*, *Eremogeton*, and probably others), the tangential pockets of radially thickened, elongate secondary phloem fibers eventually are included in the periderm. In some species certain phellem cells develop into brachysclereids.

XYLEM: Data on xylem anatomy of *Leucophyllum* kindly have been provided in part by David Michener, whose interest in *Leucophyllum* was sparked by previous studies of woods of shrubby Scrophulariaceae, namely *Keckiella* (Michener 1981). A full report on comparative xylem anatomy of *Leucophyllum* will be presented elsewhere by Michener. His data provide evidence that the woody habit of *Leucophyllum* may be secondarily derived from herbaceous ancestors.

The data on xylem anatomy were obtained from standard transverse, tangential, and radial sections and macerations from samples of each of the eight *Leucophyllum* species native to Coahuila, Chihuahua, Nuevo León, Tamaulipas, and Texas. The following summary constitutes a generic description of the xylem of *Leucophyllum*. Woods of *Eremogeton* have not been studied.

Xylem of *Leucophyllum* has both distinct and indistinct growth rings even in one stem reflecting periodic growth flushes probably tied to rainfall. Vessel elements are aggregated and widest in the initial portion of a growth ring; they continue across the growth increment as narrow elements, mostly loosely aggregated in meandering to radial chains associated with paratracheal axial parenchyma. The growth ring terminates in a narrow band of very narrow vessel elements ($\pm 12-15 \mu\text{m}$ in diameter) that can be

distinguished from fibers in cross section by their pitting. Occasional elements in this zone do not develop perforations and thus constitute vascular tracheids. Vessel elements have simple perforations. The wider elements frequently have narrow tails at one or both ends and perforations are oblique to transverse. Narrower vessel elements tend to have more oblique to nearly lateral perforations. Intervascular pitting is of alternate, circular-bordered pits. Prominent tertiary helical thickenings are frequent both in wide and narrow vessel elements. Vessel elements are short (mean lengths range from $158 \pm 41 \mu\text{m}$ to $238 \pm 51 \mu\text{m}$) and narrow to very narrow (mean diameters range from $40 \pm 17 \mu\text{m}$ to $24 \pm 9 \mu\text{m}$) in species studied.

Axial parenchyma is paratracheal, confluent, associated with the radial chains and initial aggregations of vessel elements at the beginning of the growth ring. Successive growth rings and minor growth flushes are separated by 1-celled bands of axial parenchyma. Axial parenchyma is commonly once-divided transversely and constitutes parenchyma strands.

The ground matrix of the xylem consists of masses of narrow, moderately thick-walled fiber-tracheids with distinct outer pit apertures. In the one specimen of *L. frutescens* in which they were measured they had an average length of $427 \mu\text{m}$ with a maximum length of $550 \mu\text{m}$, minimal length of $220 \mu\text{m}$ with average length 2.25 times that of the average vessel element length for the same collection.

Both uniseriate and multiseriate rays are present. Uniseriate rays are usually short, 2–3 cells tall (to 10 cells tall in *L. zygophyllum*). Multiseriate rays are 2–3 cells wide and usually less than 12 (rarely 18) cells tall. Ray cells are primarily procumbent; erect to square cells occur at the zone between successive growth increments.

Analysis of ontogenetic development of the vascular cambium of a collection of *L. frutescens* (Michener 4308) showed a drop in vessel-element length from metaxylem into the first four increments of secondary xylem. The mean vessel element length in late metaxylem was $396 \mu\text{m}$, for the metaxylem-secondary xylem transition area, $307 \mu\text{m}$, and for the first through fourth years of secondary growth, 187, 134, 163, and $137 \mu\text{m}$ respectively. The drop in vessel-element length reflects subdivision of cambial initials and the failure of the initials to elongate during secondary growth. This pattern is considered by Carlquist (1962, 1975) to be paedomorphic, and this pattern is considered characteristic of plants that are secondarily woody and derived from herbaceous ancestors. If this is the case in *Leucophyllum* the shrubby habit of *Leucophyllum* need not be considered such an anomaly in Scrophulariaceae nor indicative of relationship to the woody Myoporaceae.

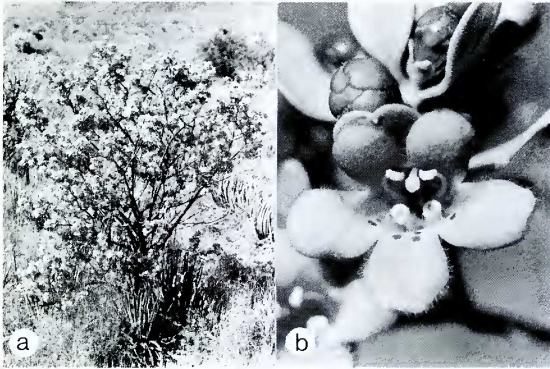


Figure 1. *Leucophyllum frutescens*. a. Habit. b. Face view of flower showing orientation of stamens, style, and spot pattern on floor of corolla throat. Note trichomes on corolla lobes, throat, and orientation of lobes in upper buds (Henrickson 19694).

LEAVES: Leaves are alternate, occasionally subopposite (when crowded), in a $2/5 - 5/13$ phyllotaxy in all species except *L. zygophyllum*, in which they are opposite, and *L. candidum*, in which they are mostly alternate but tend to be subopposite to opposite on uppermost stems. Leaves are borne only on long shoots, axillary short-shoot spurs do not form. However, axillary shoots with crowded leaves may develop in *L. minus* and *L. laevigatum* var. *griseum*. Leaves are simple, oblanceolate, obovate to orbicular, acute to rounded, emarginate at tip, narrowly to broadly cuneate or rounded at base, entire, sometimes undulate, revolute in *L. revolutum*, (fig. 2 a), toothed in *Eremogeton*, (fig. 21), flat, or conduplicately folded along the midrib in *L. zygophyllum* and *L. frutescens*, soft, pliable, mostly equally, often densely, tomentose on both sides with dendritic trichomes or less strongly vestitured on the upper surface (*L. revolutum*, *L. frutescens*) to nearly glabrous (*L. laevigatum* var. *laevigatum*, *L. langmaniae*). Stipules are absent.

Leaves of most species are isobilateral, as noted by Karrfalt and Tomb (1983), with palisade layers 2 – 5 cell layers thick on both surfaces (fig. 2 c-d), though often less well developed on the lower surface. Leaves of the bicolored *L. revolutum* and *L. frutescens* (fig. 2 a – c), as well as *Eremogeton*,

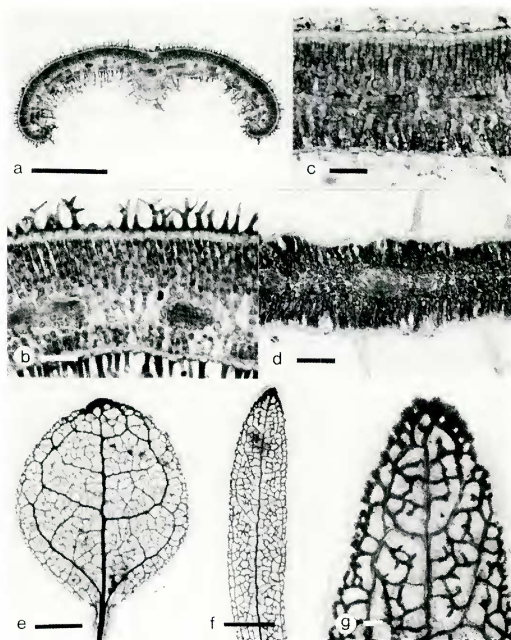


Figure 2. Leaf anatomy of *Leucophyllum*. a. Cross section of leaf of *L. revolutum* showing revolute margins and longer vestiture on adaxial surface. b. Same leaf showing short trichomes on upper surface and dorsal-ventral mesophyll structure. (Henrickson and Hess 19074). c. *L. frutescens*. Leaf cross section showing unequal development of palisade and dorsi-ventral leaf structure (Henrickson and Hess 19054). d. *L. prunosum*. Leaf cross section showing equal development of palisade in an isobilateral leaf; note also base of trichome (Henrickson and Hess 19117). e. *L. minus*. Cleared leaf with venation stained. Note venation pattern and concentration of sclerified elements near the tip. Leaf is 3.6 mm wide (Gentry 605). f.-g. *L. pringlei*. f. Cleared leaf with venation stained. g. Terminal portion of same leaf as in f enlarged, showing marginal and terminal sclerified bundle-sheath elements (tracheids) characteristic of leaves of all species (Prigge 3239). Scales in b, c, d, g = 0.1 mm; in a, e, f = 1 mm.

have a dorsi-ventral structure. The mesophyll of many species has poorly to well developed air spaces (Karrfalt and Tomb 1983, figs. 16 d, 10 a). These are lacking in *L. ambiguum*, *L. pruniosum*, and *L. pringlei*. Stomata have anisocytic subsidiary cells; some anomocytic arrangements were observed along with the anisocytic ones in *Eremogeton*. Leaves receive a single trace from a unilacunar, 1-trace node.

Cleared leaves show venation to be pinnate, camptodromous, and brochidodromous (Dilcher 1974; fig. 2 e, f, g). Secondary veins are few (2–3), abruptly curved upward near margins adjoining superadjacent secondary veins at right angles, sometimes the lowermost pair, however, do not join. Tertiary veins form orthogonal reticulæ with veins diverging at right angles from secondary and midveins. Areoles are well developed, small to medium sized (Dilcher 1974), mostly (3-)4(-5)-angled, without or with simple, linear, rarely curved veinlets (fig. 2e–g). Leaf venation is distinguished by development of groups of enlarged sclerified xylem tracheids located at tips of veinlet endings in areoles of some species and the development of larger, more conspicuous, sometimes continuous, aggregations of similar sclerified elements along the distal leaf margin, with greatest development at the leaf tip in all species. These more massive groups of sclerified cells consist of xylem tracheids and adjacent sclerified bundle-sheath elements with somewhat elongated, fully bordered pits. In some leaves layers of leaf mesophyll cells are also sclerified and exhibit small non-bordered pits. Development of marginal and terminal sclerified elements appears identical to that found in leaves of Fouquieriaceae (Henrickson 1972), where they were designated water-storage tracheids. Lersten and Carvey (1974) questioned their function in water storage in Fouquieriaceae and referred to them as sclerified veinlet elements. Their role in water transport-storage is unknown.

VESTITURE: Vestiture provides important and useful taxonomic characteristics in *Leucophyllum* and *Eremogeton*. Trichomes cover the leaves, young stems, petioles, calyces, in some species the ovary and fruit apex, style base, and various portions of the corolla. Several types of trichomes occur together in any one species.

All species have short, stipitate glands in the understory of the longer trichomes on both leaf surfaces, on calyces, and occasionally, on the stems (fig. 3 c, f, i). The trichome stalks are uniseriate, consisting of one slightly elongated or short, thick-walled cell topped with a thin-walled short cell immediately beneath the gland (fig. 3 c, i). The gland in most species of *Leucophyllum* and *Eremogeton* consists of 2 or 4 to 7 vertical cells. In *L. pringlei* the trichome gland is considerably larger and is divided vertically into 10-15 cells; the glands appear to be "sessile" but are actually short-stalked,

sunken into the leaf surface. Cronquist (1981) noted that glands divided by vertical walls are characteristic of Myoporaceae. However, nearly identical stipitate glands with glands vertically divided into 2 cells occur in *Verbascum* and other genera in Scrophulariaceae.

In *Eremogeton* trichomes on vegetative portions of the plants are uniseriate, multicellular, mostly unbranched, and typically antrorsely curved (figs. 3 g–h, 20 d). Occasional trichomes are branched and one branch may terminate with a gland (fig. 3 h). In dried specimens the thin, transparent walls of individual cells are often collapsed.

In *Leucophyllum* trichomes are once dendritically branched and consist of a uniseriate, multicellular central axis bearing 1–4 lateral, divergent, single-cell radii or “branches” at each “node” or cell junction of the central axis of trichomes in all species (fig. 3 b) except *L. pringlei*, which has multicellular lateral radii (fig. 3 d, e). Interspecific trichome variation involves the relative elongation and numbers of central-axis and branch cells. The trichomes may be very short, with short, tapering radii (*L. langmaniae*, *L. minus*, *L. laevigatum*, and some *L. frutescens*) or tall, with slender radii to 3(–5) mm long (*L. ambiguum*, *L. pruinatum*, *L. ultramonticola*) or they may have an elongate central axis with short radii (*L. candidum*). Constituent cells have clear, transparent, smooth walls that may be relatively firm and remain terete at maturity or they may be thin and collapse upon drying. The central axis may be straight or may zig-zag at the junction of each cell. Commonly tall, much-branched trichomes have no lateral branches on the lower portion of the axis (fig. 16 d). Trichome radii typically are of equal length along the axis as in the “bottle brush” trichomes on the young stems of *L. candidum* (fig. 16 ac). Occasionally, however, in *L. candidum* and others, radii on the distal portion of the trichome are distinctly shorter.

In many species young leaves are densely woolly-tomentose but vestiture is reduced in stature and density in mature leaves. This occurs partly due to the increases size of mature leaves but it is mostly because of weathering of terminal portions of individual trichomes. In instances where the more distal radii are shorter and proximal radii longer, the change in vestiture pattern, from one high stature with short radii to one of low stature with long radii on older leaves, can be considerable (fig. 16 c).

The most dramatic change in vestiture in young to old leaves is seen in *L. laevigatum* in a taxon described as *L. virescens* (= *L. laevigatum* var. *griseum*) in which young leaves are white with densely-crowded trichomes with short radii. Older leaves have a sparse vestiture of trichomes with much longer radii to 0.3(0.5) mm long (fig. 14 a, b). This apparently is not due to loss of the distal trichome radii, but, it appears that trichome radii development

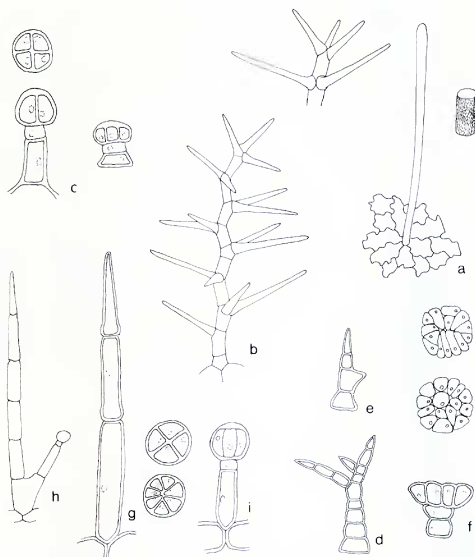


Figure 3. Trichome structure in *Leucophyllum* and *Eremogeton*. a-b. *Leucophyllum frutescens*. a. Unicellular trichome from inner floor of corolla tube. Note somewhat claviform shape, sculptured outer surface indicated in section at right. Note undulate pattern of adjacent inner corolla epidermal cells. b. Long dendritically branched trichome with 2 radii per "node" showing multicellular nature of central axis. Other trichomes may have 3-several radii per node (Henrickson and Hess 19694). c. *L. revolutum*. Glandular trichomes from leaf (left) and calyx (right). Note each consists of 2 stalk cells, the lower with thickened walls, the upper with twin walls and glandular contents. Head of glands throughout the two genera have only vertically-arranged cells, 2–15 in number. Note top view of gland with 4 cells on upper left (Henrickson and Hess 19074). d–f. *L. pringlei*. d. Branched trichome from stem showing multicellular structure. Note multicellular radii. e. Trichome with lateral protuberance accounting for branching f. Leaves have shorter, tack-shaped glands with 2 stalk cells and multicellular heads with 10–15 vertical cells arranged as shown in circular drawings above (R. Cruz C. 2008). g–i. *Eremogeton grandiflorus*. g. Stem, leaves have multicellular trichomes that typically curve distally and have collapsed walls (See fig. 20 d). h. Variation with branched trichome, one branch gland-tipped. i. Glandular trichome. Glands have 4–7 cells. Scale = 0.1 mm.

may be dependent on environment with leaves developing after rains having longer radii than those produced later in the season when conditions are drier.

Trichomes of *L. minus* (fig. 14 e, f) appear stellate but actually are only compressed dendritic with several broad, thin-walled radii extending from the tip of the central axis. Other trichomes have radii extending from the top few "nodes" of the central axis. Often in this species the terminal cells of the axis may die before differentiating and thus create a darkened, gland-appearing point at the trichome tip.

In *L. pringlei*, nonglandular trichomes are reduced and occur primarily on the stem, petioles, and occasionally along basal portions of the leaf midrib. The trichomes are uniseriate and multicellular and may be either simple or distally forked or branched (fig. 3 d, e). Trichome branching occurs either through multicellular radii or from lateral protuberances of individual cells (figs. 3 d, E; 20 c). Cell walls in this species are firm and do not collapse.

These trichome differences provide useful taxonomic characters. Trichomes of most species are illustrated with scanning electron micrographs (figs. 8, 9, 10, 13, 14, 16, 20).

INFLORESCENCES: Flowers are solitary in axils of upper leaves on terete, ascending, slender pedicels 1–5(-9) mm long in *Leucophyllum* and 2–3.5 cm long in *Eremogeton*. Pedicels are usually vestitured as the stems. In *Eremogeton*, pedicels are strongly accrescent and 4–6 cm long in fruit. Bracts and bracteoles are absent.

Leucophyllum is noted for its showy, though brief, display of flowers after rains in late summer but species occasionally flower at any time of the year. The brief display of flowers in some instances may effectively isolate sympatric species, however, simultaneous, syntopic flowering of some species can occur when the first summer rains are very late.

CALYCES: Calyces are divided into 5 lobes to or almost to the base. The tube, when present, is broadly campanulate. Calyx lobes are oblong, oblong-lanceolate to -oblanceolate, acute to obtuse at the tip, entire, slightly accrescent in *Leucophyllum*, with sessile or stipitate glands and various other vestiture (sometimes less than the subtending pedicels) abaxially and to some extent on the distal adaxial surface. Sepals of *Eremogeton* are large, oblong-oblanceolate, green, leafy, vestitures as the leaves, and accrescent.

COROLLAS. Corollas in *Leucophyllum* are sympetalous, horizontally oriented, slightly zygomorphic, (4-)5(-6)-lobed. Corolla lobes are orbicular or broader than long, mostly emarginate to rounded, entire, occasionally erose. The posterior 2 lobes are external in bud (fig. 1 a) and reflexed at anthesis. The anterior 3 lobes are spreading to reflexed-recurved with the

medial lobe larger than the lateral two and all are slightly larger than the posterior two. Externally corollas may be glabrous to sparsely stellate or stipitate-glandular. Inner corolla surfaces may have short to long, tangled, unicellular trichomes 0.2–3 mm long with blunt, rounded tips and warty surfaces (fig. 3a) located on the throat floor, sometimes also on the throat roof, and sometimes extending to lobes; in some specimens they are restricted to the lobe margins.

Corollas range from lavender, pinkish, violet to white (albino), and most have a white patch on the floor of the throat beset with irregular rows of yellow to yellow-brown spots (fig. 1 b), or they may be of a solid color or with a white patch with dark purple-violet spots. The spots apparently serve as nectar guides.

Corollas of *Eremogeton* are very large (6–7 cm long), 5-lobed (fig. 21); the lobes are oblong with the posterior 2 lobes united nearly to the obtuse to acute tips. The posterior 3 lobes are reflexed to spreading. Corollas are stipitate-glandular outside and weakly so inside. The lobes are ciliate with long, crinkled trichomes. The corollas are thick and whitish; according to label data, they open in the evening.

ANDROECIA: *Leucophyllum* typically has 4 didynamous (rarely 3 or 5) stamens. Rarely a medial, posterior staminode is present. Filaments are adnate to the corolla tube for one-fourth to one-third their total length. They may be glabrous or pilose at the base but are glabrous and whitish where free above. In the species descriptions the filament lengths recorded are measured from the base of the corolla to the anthers because insertion is often variable even in an individual flower. Filaments of the posterior stamens extend along the upper margin of the tube-throat and abruptly turn inward just below the anther; the anthers are positioned along the roof of the mouth (fig. 1b). The relatively shorter filaments of the anterior stamens extend along the margin of the corolla tube floor and turn inward just below the anthers, which are then situated at the floor of the corolla mouth (figs. 1 b, 19 d). Anthers are white to yellowish, glabrous, bithecal but 3-locular (fig. 5 q), with the inner 2 locules shorter and distinct while the outer anther sac is longer, confluent across the anther tip. Dehiscence occurs between the inner and outer anther locules, and after anthesis the anther sacs are explanate, divergent 120–180 degrees (fig. 5 q).

Eremogeton, in contrast, has only the two anterior stamens, (the two posterior stamens are sometimes represented as filamentous staminodia) with glabrous, whitish filaments inserted at the base of the corolla tube and anther sacs exerted and situated below the two posterior corolla lobes. The whitish anthers sacs are similar to those of *Leucophyllum* but are divaricate only 30–40 degrees after pollen release.

Pollen in all species is distinctive, 3-colporate, diorate, with mesocolpia reticulate, tectate, and exhibits some variation in sculpturing (Niezgoda & Tomb 1975). Pollen grains of *Leucophyllum* range from 21–26 μm in equatorial diameter, 19–30 μm in polar diameter (Niezgoda & Tomb 1975). Those in *Eremogeton* are similar but slightly larger (30.6–31.6 μm).

GYNOECIA: Ovaries are superior, 2 (rarely 3)-carpelled, 2(-3)-loculed, with expanded, axile, medially-furrowed placentae (figs. 4 c, d; 5 q). Ovules are numerous in each locule, borne on the expanded placentae, campylotropous (fig. 5 n), tenuinucellar, and unitegmic. The styles are terminal, cylindrical, and glabrous or variously vestitured at the base. The style tip expands into a slightly flattened, acute to rounded, mostly rhomboid, thickened tip that is papillate and stigmatic across the distal margin (or margins when acute). There is some interspecific variation in stigma structure; some species have blunt tips, others have more elongate, acute tips that sometimes fold back upon drying.

FRUITS: Fruits are woody capsules that dehisce septically to the base and part way to the base loculicidally. The outer 3–5 layers of the fruit wall consist of soft cells; the inner 3–4 layers consist of radially oriented lignified sclereids with the innermost sclerified layer parallel to the inner carpel wall surface (fig. 4 d, e). Fruits are contained within the persistent, slightly accrescent calyx and may be glabrous or glabrate or persistently beset with dendritic trichomes near the tip. Capsule structure is basically identical to that found in *Penstemon* (Scrophulariaceae).

SEEDS: Seeds are small, often somewhat flattened, angular, in *Leucophyllum frutescens* 1–1.3 mm long, 0.5–0.7 mm wide, mostly 0.2–0.5 mm thick with shape affected by the close packing of the seeds between the expanded axile placentae and the ovary wall (fig. 4 f). Testa are brown to gray with a reticulate pattern formed as tangential walls collapse between erect radial walls (fig. 4 g). The embryo occupies about 80 percent of the seed, is 0.8–1.1 mm long, flattened, and has two oblong cotyledons that are rounded at the tip and are about equal in length to the hypocotyl. Endosperm is about 0.1–0.15 mm thick and consists of 3–5 layers of cells with unevenly thickened walls. Both endosperm and embryo contain oil droplets that stain with Sudan IV. Seeds are identical to those sampled in *Penstemon* and *Verbascum* except for the convoluted external sculpturing in the latter. Seeds of *Eremogeton* are similar in structure but slightly larger.

FLOWER VASCULARIZATION: Flower vascularization of *Leucophyllum* was studied from serial sections and clearings of whole flowers (figs. 4 b–d, 5 a–p). Pedicels contain a continuous cylinder of vascular tissue (fig. 5 a). Ten vascular traces emerge in one series in the receptacle: five medial sepal

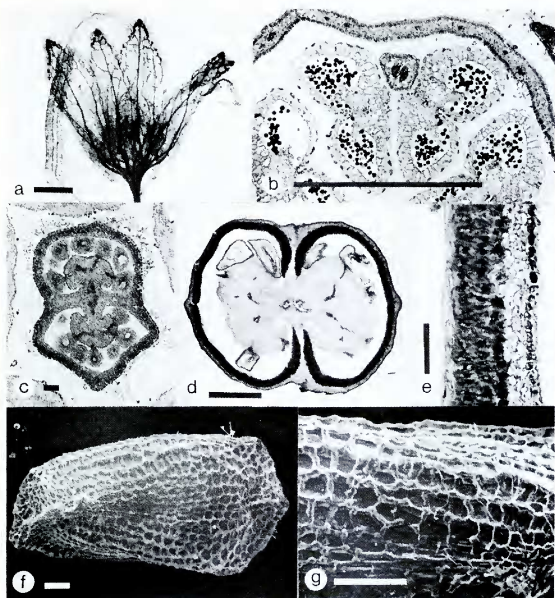
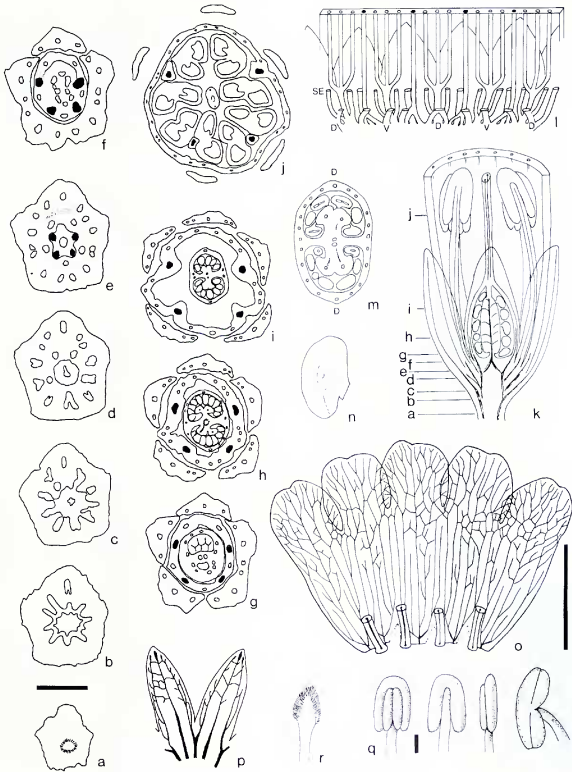


Figure 4. Floral, fruit, and seed structure of *Leucophyllum*. a. *L. frutescens*. Cleared flower, note vascularization and sclerified elements at tip of sepals (Henrickson and Hess 19054). b. *L. prinosum*. Cross section of anther below attachment of filament showing 4 locules, corolla (Henrickson and Hess 19117). c. *L. revolutum*. Cross section of ovary showing axial placentation. Ovary is 1.26 mm long (Henrickson and Hess 19074). d-e. *L. frutescens*. d. Cross section of fruit note locatin of sclerenchyma in fruit wall and axial placentae with few developing seeds. Ovary is 4 mm long. e. Enlargement of fruit wall showing epidermis, (on right), few parenchyma layers and (on left) inner layer of 3 radial and innermost tangentially-elongated sclerenchyma cells. Structure is identical to that found in Scrophulariaceae (Henrickson and Hess 19054). f-g. *L. frutescens*. f. SEM of seed, note surface sculpturing. g. Enlarged view of seed surface showing reticulate pattern developed by collapse of tangential epidermal walls (Henrickson and Hess 19301). Scales in a, b, d = 1 mm; in c, e, f, g = 0.1 mm.

traces alternate with five petal-sepal traces. The petal-sepal traces soon branch off two lateral traces, one going to each adjacent sepal as lateral sepal traces. The remaining adaxial vascular tissue then continues as the petal trace (fig. 5 b - d, 1). Each sepal then receives three separate traces (fig. 5 p) that branch and anastomose distally in the lobes. They are associated with sclerified bundle-sheath cells similar to those in the leaves (figs. 4 a, 5 p). Similar thickenings also occur along the thickened basal portions of the sepal traces (figs. 4 a, 5 p). The remaining five petal traces each branch into three traces at the base of the corolla tube and continue to branch and anastomose further up the corolla tube and into the lobes (fig. 5 o). After the sepal and petal traces diverge, the remaining receptacular vascular tissue forms into a cylinder giving rise to the four stamen traces (shown in black in fig. 5 g - j). These merge into the corolla, eventually becoming free some distance above the corolla base. The remaining vascular tissue organizes into the ovary traces. That portion of the vascular tissue that would have gone to the posterior or fifth stamen develops into the dorsal trace of the posterior carpel thus affecting the vertical orientation of the ovary. The remaining vascular tissue forms into the other dorsal, ventral, and lateral traces, with the dorsal traces continuing into the style (fig. 4 a). The pattern illustrated in fig. 5 a - 1 was found in all flowers of *Leucophyllum* studied, except in one flower of *L. frutescens* in which the lateral sepal traces of two sepals developed from the medial sepal trace rather than the alternate petal traces. The vascularization pattern was identical to that found in both

Figure 5. Flower vascularization and structure of *Leucophyllum*. a - j. Diagrams of vascular system as seen in serial cross sections of *L. pruinatum* at levels indicated in k. Stamen traces are indicated by black circles. Note sepals receive 3 traces, medial traces directly from receptacle, lateral traces branch from adjacent petal traces. Also note origin of stamen traces (Henrickson and Hess 19117). k. Cutaway longitudinal diagram of flower showing patterns of vascular bundles in receptacle and approximate levels of sections a - j. l. Two-dimensional diagram of vascular system as seen from inside flower cut between anterior lobes, with lowest, innermost series of traces going to ovary (D = dorsal traces, V = ventral traces), second series to sepals (SE), note medial trace develops directly, lateral sepal traces develop with petal traces. Petal traces branch at corolla base, stamen traces terminate with black circles. m-r. *L. frutescens*. m. Cross section of ovary showing 2 carpels, dorsal traces (D), expanded axile placentae, ovules. n. Camplyotropous ovule (diagramatic). o. Vascular system of corolla as seen from adaxial surface cut between 2 posterior lobes. Note basal branching of initial 5 petal traces and basal portion of 4 stamens. p. Vascular system of mature calyx showing 3 traces, distal trace branching and location of sclerified elements near sepal tip. q. Anther structure as seen from adaxial (left), and abaxial side views and after anthesis (right). Note outer thickened is continuous around 2 inner locules. r. Style tip showing marginal papillate thickened stigmatic portion (m-r from Henrickson and Hess 19074). Scale above a = 1 mm holds for a-j; in o = 1 cm; in q = 1 mm.



Penstemon and *Myoporum laetum* except for the 3-carpelled gynoecium and reduced ovule number in the latter. Vascularization of flowers of *Eremogeton* was not studied as no material was available.

CYTOLOGY

Flyer (1970) reported one unvouchered chromosome count for *Leucophyllum* ($n = 15$, for *L. minus*). He noted that meiosis apparently is very rapid in pollen parent cells, for, despite numerous attempts, no stages between prophase and the tetrad stage could be seen with this one exception. The number $\underline{n} = 16$ may reflect $\underline{x} = 8$; $\underline{x} = 8$ has been reported for other Scrophulariaceae (e.g., some species of *Verbascum* and *Mimulus* and throughout the genera *Antirrhinum*, *Pedicularis*, and *Penstemon*). Myoporaceae has $\underline{x} = 18$ in *Eremophila*, (Barlow 1971) and $\underline{x} = 27$ in *Myoporum* (Hair and Beuzenberg 1959).

SPECIES RELATIONSHIPS

Various phenetic and cladistic analyses were performed on character data obtained from *Leucophyllum* species. Problems arose with characters involving vestiture. Plants with dense stem-leaf vestiture had an uneven and apparently meaningless, though species-specific, continuation of vestiture onto various floral features. Certain species, however, grouped together in most analyses, including: (1) *L. ambiguum*, *L. ultramonticola*, *L. pruinosum*; (2) *L. laevigatum*, *L. griseum*, *L. minus*; and (3) *L. zygophyllum*, *L. candidum*. *Leucophyllum pringlei* usually did not group closely with other species. The positions of *L. frutescens*, *L. revolutum*, *L. langmaniae*, and particularly *L. flyrii* were very variable. Use of different or reduced data-sets gave variable results but from this came a synthesis of data resulting in a tentative tree (fig. 6), derived by applying the method of grouping of species by shared derived character states (synapomorphies). This is presented in the form of a cladogram to facilitate representation of character states in relation to proposed relationships. The basic structure of the tree was derived from a reduce data-set using only 11 characters but these characters are considered to be significant. Relationships at some upper points of the tree were resolved through other data-sets. Attempts to apply the outgroup method (Stevens 1980) of character polarization were largely unsatisfactory. Relationships undoubtedly lie within Scrophulariaceae but exactly where is not known. However, as all species of *Leucophyllum* are woody, have some form of branched, dendritic vestiture, have glands with 2 stalk cells and multicellular gland heads with vertically-oriented cells, have bractless, ebracteolate flowers with 5 subequal corolla lobes, (the posterior 2 lobes external in bud), and have 4 anthers with continuous outer thecae and bicarpellate

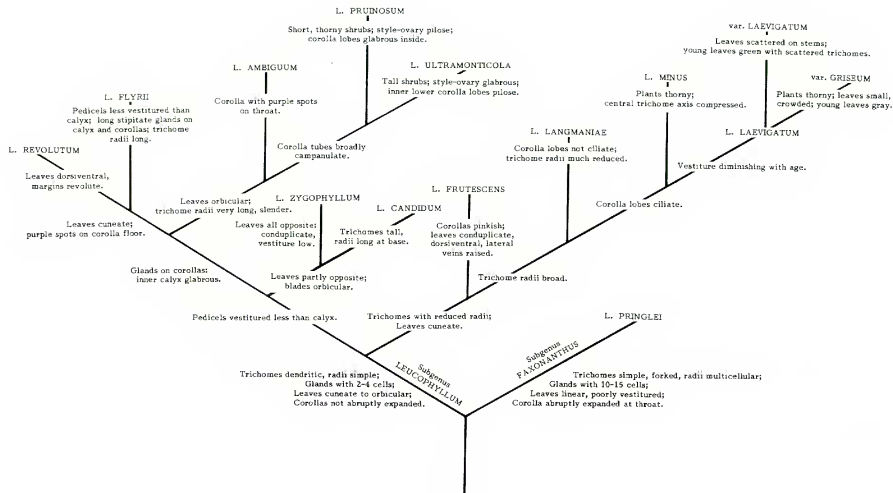
ovaries with axial placentae, etc., these characters are considered to be primitive (plesiomorphic) for the genus. Factors such as thorny, reduced habit and degrees of vestiture development are considered to be highly variable and poor characters for estimating (guessing at) phylogeny. The pattern that emerges from phytogeographic evidence (see below) is that *Leucophyllum* may be an old group that has been in existence in the altiplano of Mexico in arid and semiarid habitats since perhaps the late Eocene (Axelrod 1979) and its history may be marked by hybridization (as is occurring today) with derivatives recombining characteristics and thus its phylogenetic history may include reticulations between major lines.

In figure 6, trichomes of moderate stature with single-celled, moderate-lengthed radii, cuneate, alternate leaves, and yellow corolla-throat spots are considered plesiomorphic. From these states, opposite, linear or orbicular leaves with either very long or reduced vestiture with very long and slender or short radii and development of purple or no corolla throat spots are considered derived. Vestiture types appear to have evolved more than once. Vestiture varies throughout the range of *L. frutescens* from very tall to highly reduced and obscure. In its reduced state the vestiture is very similar to that found in *L. langmaniae*, which we do not, however, consider to be closely related. Corolla throat spotting varies throughout the range of *L. ambiguum*. Most populations have no corolla spots but collections near Meztitquitlan in Hidalgo have yellow corolla-tube spots—is this an atavistic or apomorphic feature? Data summarized in fig. 6 must be considered tentative but reflective of possible relationships of the taxa of *Leucophyllum*. Our biggest questions concern relationships of *L. flyrii*. It is similar to *L. revolutum* in its cuneate leaves and purple corolla spots but, unlike *L. revolutum*, its leaves are isobilateral not dorsi-ventral. It also shares characteristics with members of the *L. ambiguum-pruinatum* complex, which can also have purple spots on the corolla floor, isobilateral (but orbicular) leaves, and long trichome radii.

Eremogeton, with its large, toothed leaves and large white, more strongly zygomorphic flowers with only 2 stamens, is considered to be distinct from the hypothetical ancestor of *Leucophyllum*. It is not included in this discussion. Because of the large number of apomorphic features that distinguish *L. pringlei*, it is here considered as a distinct subgenus.

PHYTOGEOGRAPHY

Leucophyllum is one of several genera endemic to the arid and semiarid regions of Mexico and adjacent United States (Rzedowski 1962, 1973). Axelrod (1979) considered *Leucophyllum* among those genera that evolved autochthonously in this region, perhaps from ancestors present during late Cretaceous-Paleocene times (50–60 mybp) that initially adapted to local



semi-arid sites and became adapted to the more arid climate that arose in late Eocene and later times. A possible scenario for development of the genus involves the development of arid zones in central Mexico from Tertiary onward. In early Tertiary local dry sites were scattered all across central Mexico in the lee of mountains allowing plants to gradually adapt to these sites (Axelrod 1979). During Eocene, the uplift of the Sierra Madre Oriental and other parallel ranges in central Mexico (the Hidalgoan Orogeny of de Cserna; see de Cserna 1960; Guzman, and de Cserna 1963) and additional volcanism resulted in a more widespread development of arid sites throughout Mexico. Much later in Miocene-Pleistocene, development of the igneous-rock Sierra Madre Occidental caused still further expansion of these arid and semi-arid zones throughout central Mexico and allowed taxa to adapt to arid- and semi-arid habitats to spread throughout the expanded dry zone that extended from Puebla to northern Mexico. Vegetation in the Miocene and early Pliocene in central Mexico, which according to Axelrod (1979) probably was warmer and had higher precipitation than today, may have consisted of dry tropical forests and woodland with thorn scrub and drier edaphic and lee-slope-habitats supported semi-arid taxa. During late Pliocene to Recent time extensive volcanic activity formed the trans-volcanic belt (Guzman and de Cserna 1963) which isolates the Pueblan arid zone (present home of *L. pringlei*) from those in the north; later uplifting and volcanic activity isolated the Hidalgoan arid region from that of the Chihuahuan Desert Region in the north (Axelrod 1979). While the southern Puebla arid regions were protected from cold winter northern fronts by the trans-volcanic belt, species diversity in the northern Chihuahuan Desert was impoverished by increasingly colder climates particularly during Quaternary glacial periods. During the Quaternary these semi-arid and arid zones were alternately reduced and expanded during pluvial and interpluvial periods. Van Devender (1977) noted that during the latest pluvial period pinyon-juniper-oak woodland vegetation extended into the areas now occupied by the northern Chihuahuan Desert, which expanded to its present conformation only within the last 8000 (-4000) years.

With the absence of fossil evidence it is not possible to know exactly how *Leucophyllum* and *Eremogeton* fit into such a scenario. Consideration that the nearest relatives of these genera of Scrophulariaceae have always been considered to be Old World herbaceous and suffrutescent genera implies that *Leucophyllum* and *Eremogeton* may be New World vicariants or at least

Figure 6. Diagram of an intuitive phylogeny of the species of *Leucophyllum*. See text for explanation.

New World survivors. Michener's xylem ontogeny data indicate that the shrubby habits of our taxa may be a derived condition. *Leucophyllum* particularly appears to be well adapted to arid and semi-arid habitats in central Mexico exhibiting a number of xeromorphic features and, undoubtedly, a number of physiological features that allow it to survive in these environments.

The present distribution of taxa appears to fit well into a vicariance model. The distinctive *Eremogeton* is geographically well isolated from the more northern species of *Leucophyllum*. *Leucophyllum pringlei*, which here is considered to be the sole member of a separate subgenus, occurs in Puebla and Oaxaca, south of the late-Pliocene-Recent Trans-volcanic belt. The other species of *Leucophyllum* occur north of this volcanic axis, one in Hidalgo-Querétaro, the others in or around the Chihuahuan Desert. These eleven species show various distribution patterns in related lines. The three species with long trichome radii (*L. ambiguum*, *L. pruinosum*, and *L. ultramonticola*) seem to form a related group and are widely disjunct: *L. ambiguum* occurs in the southern disjunction of the Chihuahuan Desert in Hidalgo and Querétaro, *L. pruinosum* in basins in southern Nuevo León and adjacent Tamaulipas and San Luis Potosí, and *L. ultramonticola* in an arid pocket along the Rio Atengo in Southeast Zacatecas (fig. 16). Their present ranges probably reflect their respective refugia during the past pluvial period. It is of course attractive to propose that they may have been one widespread species during the previous interpluvial period and that subsequent isolation of refugial populations resulted in the differentiation of these three closely related vicariant species.

Many of the present day species of *Leucophyllum* occur in a Chihuahuan Desert scrub, mostly in a mixed desert scrub association above the *Larrea* zone up to the *Yucca-Dasyliirion*-dominated zones; their ranges were probably restricted during the latest pluvial period, or at least they were restricted to arid habitats within the presumed dominant woodland communities. The presumed bottlenecks in population size could well provide for more rapid character differentiation that is reflected in today's more expanded populations. At present, populations of *L. candidum*, *L. minus*, and, particularly, *L. frutescens* seem to be expanding their ranges. The latter species appears to be expanding northward from a potential refugium east of the Sierra Madre Oriental into southern Texas and spilling over into the Chihuahuan Desert. The occurrence of three species of *Leucophyllum* in the basins around southern Nuevo Leon separated from the main mass of the Chihuahuan Desert by series of low mountains is of considerable interest. This area may well have served as a refugium during the past pluvial period:

it is the present-day home of *L. pruinatum*, *L. revolutum*, and *L. zygophyllum*. Many other endemics also occur in this area.

Three species of *Leucophyllum* appear to be relictual and occur only in reduced populations. *Leucophyllum langmaniae* occurs in isolated arid pockets in the woodlands in canyons between Monterrey, Nuevo León, and Saltillo, Coahuila. The geographical extent of this species is not known. *Leucophyllum flyrii* is known only from two populations, one near Laguna Seca (Gral. Candido Navarro) and one in the adjacent sierras in central San Luis Potosí. The extent of *L. ultramonticola* in southwestern Zacatecas is unknown.

ECONOMIC USE

Leucophyllum frutescens is commonly cultivated and is known as cenizo, ceniza, Texas silverleaf, Texas ranger, purple sage, and, less frequently, barometer bush, liar bush, ash bush, Texas rain sage (Texas Agricultural Experiment Station Tract L-2058). The species has been widely cultivated in south-central Texas and is becoming popular throughout the Southwest in relatively frost-free, arid regions. The plants can, however, tolerate light to moderate frost. The species is popular because of its white-gray foliage, rounded habit, and great show of pink-purple flowers after rains in late summer-fall. According to the Texas Agricultural Experiment Station, the plants prefer open sun and alkaline soils with good drainage. Recently the Texas Agricultural Experiment Station has made available a white-flowered, gray-leaf cultivar 'White Cloud,' and a green-leaved, purple-flowered cultivar 'Green Cloud' of *L. frutescens*, and a deep violet-flowered, gray-leaved cultivar of *L. candidum* under the name 'Silver Cloud.' Plants are propagated by cuttings. Flowering plants may be produced from seeds in about two years.

TAXONOMIC TREATMENT

- A. Corollas 60–70 mm long, white, posterior 2 lobes united to near tip, erect, anterior 3 lobes oblong-ovate, spreading, 25–33 mm long, 13–15 mm wide; calyx lobes 2–3.6 cm long, 4–7 mm wide; stamens 2; trichomes multicellular, tapering, antrorsely curved; leaves 4–12 cm long; México (Chiapas) and Guatemala II. *Eremogeton*. *E. grandiflorus*
- AA. Corollas 8.5–28 mm long, lavender, violet, pinkish, rarely white (albino), often with white on floor of tube marked with yellow or purple dots, lobes all orbicular to broadly oblong, subequal, 3–10 mm long and wide; calyx lobes 5–10 mm long, 0.7–1.5 mm wide; stamens 4, didynamous; trichomes multicellular, erect, stellate or dendritic or forked distally; leaves 6–35 mm long; México (Oaxaca) to sw. U.S. I. *Leucophyllum*
- B. Leaves linear-lanceolate, 6–12 mm long, 1.2–2.2 mm wide, crowded, glabrous except for sessile glands; young stems with erect,

- tapering or distally forked trichomes 0.1–0.25 (–0.4) mm long; Puebla and Oaxaca. 12. *L. pringlei*
- BB. Leaves oblanceolate, obovate to orbicular, mostly 2.5–12(–22) mm wide, tomentose or with scattered stellate or dendritic trichomes; young stems canescent to tomentose with stellate to dendritic trichomes; Hidalgo and northward.
- C. Leaves bicolorous, upper leaf surfaces more green with slightly to much-reduced vestiture (be sure to look at both surfaces of one leaf).
- D. Leaf blades oblanceolate, 2–4(–5) mm wide, at margins distinctly revolute, often inrolled towards leaf base; corollas violet with dark violet spots inside on floor of tube; sw. Tamaulipas to adjacent n. San Luis Potosí. 7. *L. revolutum*
- DD. Leaf blades obovate to oblong-obovate, (4)6–16 mm wide, margins flat or variously undulate, not revolute; corollas pinkish to lavender, with yellow spots inside on floor of tube; w. central Texas s. to e. central Coahuila, Nuevo León, s. Tamaulipas. 1. *L. frutescens*
- CC. Leaves concolorous, upper and lower surfaces equal in vestiture and color (although sometimes more strongly vestitured along midrib beneath).
- E. Vestiture of leaves and young stems densely and closely silver-gray canescent, trichomes crowded, overlapping, appearing stellate, radii broad, translucent to whitish, to 0.1 mm long, radiating from a central, often gland-tipped, axis (use 30 X magnification); leaves small, crowded at nodes; thorny shrubs from sw. New Mexico through Trans-Pecos Texas to e. Chihuahua, s. to about 50 km ne. of Saltillo, Coahuila. 3. *L. minus*
- EE. Vestiture of at least young stems and often of lower leaf margins of dendritic trichomes, this often of an uneven stature, or if not, then either older leaves greenish or trichome arms slender, longer.
- F. Leaf-blades mostly ovate-orbicular, abruptly narrowed at base; petioles usually conspicuous; leaves silver-gray.
- G. Leaves all opposite, usually conduplicately folded along midrib; leaf-blades commonly orbicular or nearly so, closely vestitured; s. Nuevo León, sw. Tamaulipas and adjacent San Luis Potosí. 6. *L. zygophyllum*
- GG. Leaves mostly alternate, occasionally some leaves opposite or sub-opposite, seldom conduplicately folded; leaf-blades orbicular or not, with dense, thick vestiture.
- H. Corollas uniformly violet to purple throughout, occasionally with white along very base of tube but without colored dots in lower tube; Hidalgo to Querétaro. 11. *L. ambiguum*
- HH. Corollas lavender to violet but with lighter or white patch on floor of tube marked with yellow or deeper violet spots; plants of more northern distribution.

- I. Dendritic trichomes of young stems and leaf blades long and slender, mostly 0.1–0.5 mm in diameter with radii 0.1–0.25 mm long, only a few times longer than the thickness of the trichome axis; compact shrubs of Brewster Co., Texas, s. through central Coahuila to Zacatecas, e. Durango, central Chihuahua. 5. *L. candidum*
- II. Dendritic trichomes of stems and leaf-blades 0.3–1.5 mm in diameter, with radii (0.1–) 0.2–0.5(–8) mm long, many times longer than the thickness of the axis; shrubs from s. Nuevo León to Zacatecas.
 - J. Style, ovary, and capsule tip glabrous or with few glands; corolla lobes pilose inside; sw. Zacatecas. 10. *L. ultramonticola*
 - JJ. Style, ovary, and capsule tip pilose to densely pilose; corolla lobes glabrous inside; s. Nuevo León, adjacent Tamaulipas, San Luis Potosí. 9. *L. pruinosum*
- FF. Leaf-blades obovate-oblancoolate, cuneate, gradually narrowed to base; petiole (if present) not conspicuous; leaves green or not.
 - K. Calyx lobes with scattered long-stipitate glands extending well above the vestiture; corolla with dark purple (not yellow) dots on floor of tube inside; leaves permanently gray-canescens; ne. of city of San Luis Potosí. 8. *L. flyrii*
 - KK. Calyx lobes lacking long-stipitate glands; corollas with yellow dots on floor of tube inside; mature leaves often greenish.
 - L. Leaves appearing glabrous but uniformly covered with relatively dense, but minute trichomes to 0.05 mm wide on both surfaces; radii about as long as central trichome axis; corolla lobes not ciliate; local between Monterrey, Nuevo León, and Saltillo, Coahuila. 2. *L. langmaniae*
 - LL. Leaves with scattered to dense, stellate trichomes 0.1–0.2 (–0.8) mm broad; radii mostly 2 times longer than trichome axis; leaves either green or the youngest leaves (occasionally all) gray; corolla lobes distinctly ciliate; plants from Chihuahua and Coahuila, to San Luis Potosí, Durango, and Zacatecas. 4. *L. laevigatum*

I. LEUCOPHYLLUM Bonpl. in Humb. & Bonpl., Pl. Aequinoct. 2:95. 1812. TYPE: *Leucophyllum ambignum* Bonpl. in Humb. & Bonpl.

Terania Berlandier, Mem. Com. Limit. Mier y Teran 4. 1823. TYPE: *Terania frutescens* Berlandier.

Rounded to rhomboid, moderately to strongly branched, evergreen to semi-deciduous, silvery-gray to greenish shrubs; young stems subterete, uniformly to irregularly tomentose to canescent with stellate to dendritically-branched, rarely forked, spreading trichomes, in age more uniformly tomentose-canescens due to weathering, eventually glabrate;

older stems with dark to light gray or reddish-brown, smooth or vertically fissured bark; older dead stems sometimes persisting as thorns. Leaves alternate, subopposite to opposite, simple, often crowded or sometimes also in reduced subfasciculate, axillary shoots, oblanceolate, obovate, elliptical, orbicular to ovate-orbicular, obtuse, rounded to acute or emarginate, with midrib continuing as a blunt, sometimes reflexed apiculation at tip, cuneate, sessile or subsessile to abruptly cuneate-rounded and distinctly petiolate at base, entire to revolute, often somewhat conduplicate folded along midrib or otherwise undulate, soft, pliable but usually thickish due to thick indumentum, silvery-gray to greenish, densely tomentose to canescent or sparsely vestitured with dendritically-branched or stellate trichomes, rarely glabrous. Trichomes uniform on both surfaces or shorter or more sparse above, consisting of a series of long, slender or short, tapering, straight or wavy simple radii extending from a short to elongated multicellular central axis that may fragment causing a reduction in vestiture stature through a season, mostly with sessile to stipitate glands in understory, with midrib and sometimes secondary veins raised beneath, abscissing above prominent, usually persistent leaf bases. Flowers 1(-2) in axils of leaves, mostly produced in abundance after rains; bracts, bracteoles absent; pedicels ascending, vestitured as young stems; calyces divided to near base into 5 lobes, lobes lanceolate to oblong-ovate, acute to attenuate, valvate in bud, tomentose, canescent as leaves or young stems or with a diminished vestiture, obscurely glandular, rarely long stipitate-glandular outside, glabrous, glandular or sericeous or sparsely stellate except a tip inside; corollas showy, lavender, light violet to pink-lavender, blue, violet, rarely white, mostly with one or more white patches on floor of tube marked with rows of yellow-brown to orange dots, or of a solid color marked with dark purple-violet spots, zygomorphic, funnelform to campanulate, tube gradually to abruptly ampliate, usually slightly to moderately dorsiventrally compressed, lobes (4-)5(-7), shorter than tube, imbricate in bud, spreading, posterior two sometimes more reflexed than anterior three, often with long, slender, angled unicellular trichomes on floor of tube and on lower throat, with straight, erect, slightly clavate, colored hairs on throat and often on inner surface and margins of lobes, glabrous to sparsely glandular-pilose, rarely sparsely stellate outside; stamens (3-)4(-5), didynamous, included or the longer, posterior pair slightly exerted; filaments adnate to base of corolla tube for one-fourth to one-third length, glabrous or pilose near base, cylindrical to slightly compressed, whitish above, posterior pair spreading, inwardly curved at tip, anterior pair upwardly curved at tip; anthers white to yellowish, glabrous, anther sacs becoming widely divaricate ($120 - 180^\circ$), outer locules confluent, inner locules distinct, dehiscent across continuous end, promixal anthers oriented parallel to tube axis, anterior pair oriented nearly perpendicular to floral axis; ovary superior, ovoid, glabrous or pilose or loosely stellate at tip, 2-loculed; placenta oblong, attached medially along septum; ovules many;

styles terminal, cylindrical, glabrous to sparsely pilose, straight, extending to posterior corolla tube-throat, sometimes slightly exerted, decurved at tip, flattened, stigmatic along distal margin of terminal, obtuse to somewhat acute tip. Fruit of dark brown, woody, ovoid, apiculate capsules, these dehiscent first septically to near base, then loculicidally half way to base, enclosed in slightly accrescent calyx; seeds 15–25 per locule, small, irregularly ovoid, yellowish-brown, minutely reticulate, smooth to somewhat angled. Chromosome number $n = 16$ (one species).

LEUCOPHYLLUM Bonpl. in Humb. & Bonpl. subgen. LEUCOPHYLLUM.

Trichomes dendritic, with unicellular radii; glandular trichomes with 2–7 cells in head; leaves oblanceolate, obovate to orbicular, mostly covered with trichomes on both surfaces.

Distribution: Texas, adjacent New Mexico, south from Chihuahua and Tamaulipas to San Luis Potosí and Zacatecas, also in Hidalgo and Querétaro. (Species No. 1–11).

LEUCOPHYLLUM Bonpl. in Humb. & Bonpl. subgen. *Faxonanthus* (Greenman in Sargent) Henrickson & Flyr, comb. et stat. nov. *faxonanthus* Greenman in Sargent, Trees & Shrubs 1:23. pl. 12. 1902. TYPE: *Faxonanthus pringlei* Greenman in Sargent.

Trichomes simple or distally forked, with multicellular radii; glandular trichomes with 10–15 cells in head; leaves linear-lanceolate, glabrous except for sessile glands.

Distribution: Southern Puebla and adjacent Oaxaca. (Species No. 12)

1. LEUCOPHYLLUM FRUTESCENS (Berlandier) I. M. Johnston, Contr. Gray Herb. 70:89. 1924. *Terania frutescens* Berlandier Mem. Com. Limit. Mier Y Terán 4. 1832. TYPE: MÉXICO. NUEVO LEÓN: Monterrey, *Berlandier 1406* (LECTOTYPE: BM!; ISOTYPE: OXF!)

Leucophyllum texanum Benth. in DC., Prodr. 10:344. 1846. TYPE: TEXAS. WEBB Co.: "Laredo," *Berlandier 2070* (LECTOTYPE: here designated K!).

Leucophyllum frutescens (Berlandier) I. M. Johnston forma *albiflorum* Clover, Madroño 4:97. 1937. TYPE: TEXAS. STARR CO.: Roma, *Clover 492* (HOLOTYPE: MICH!)

Leucophyllum frutescens (Berlandier) I. M. Johnston forma *albivium* Lundell, Contr. Univ. Mich. Herb. 8:86. 1942. TYPE: TEXAS. CAMERON CO.: 8 mi W of Boca Chica, 12 Mar 1942, C. L. Lundell and A. A. Lundell 10699 (HOLOTYPE: MICH!; ISOTYPES: LL!, TEX!).

[*Leucophyllum frutescens* (Berlandier) I. M. Johnston var. *floribunda* R. A. Vines, *nom. nud.* Trees, shrubs, and woody vines of the southwest p. 920. 1960.]

[*Leucophyllum frutescens* (Berlandier) I. M. Johnston var. *glaucom* R. A. Vines, *nom. nud.* Trees, shrubs, and woody vines of the southwest p. 920. 1960.]

Erect, rounded, alternately-branched shrubs 0.5–2(–3) m tall; young stems densely tomentose with conical to cylindrical, dendritic trichomes

0.1–0.3 mm long with short tapering radii 0.05–0.1 mm long, tardily glabrate; older stems with reddish-brown to light-gray bark. Leaves alternate, rarely opposite, obovate, oblong-obovate, to obovate-orbicular, 10–25(–35) mm long, (4–)6–16 mm wide, obtuse, rounded, often bluntly apiculate at tip, cuneate to petiole 1–2 mm long at base, at margins entire, sometimes slightly revolute, usually conduplicateley folded along midrib, mostly silvery-gray, tomentose on both surfaces but with shorter, more open vestiture and more gray-green to green above, upper surface with dendritic trichomes 0.1–0.3 mm high or mixed dendritic and shorter stellate trichomes or rarely of reduced, scattered stellate trichomes to 0.1 mm long, sometimes appearing nearly glabrous except for glands, lower surface mostly densely, irregularly tomentose with dendritic trichomes 0.2–0.3(–1.0) mm high, radii mostly straight, slender, 0.1–0.2 mm long, midvein and secondary veins raised beneath. Flowers with tomentose pedicels 1–4 mm long; calyces 5–7 mm long, lobes oblong-lanceolate, 3–5 mm long, 1.3–2.1 mm wide, acute, densely tomentose with dendritic trichomes as on stem outside, more glabrous, strigose slightly glandular in lower half inside, to 6 mm long, 2.5 mm wide in fruit; corollas rose-lavender, light violet, rose-pink to reddish-pink (rarely white), with white patch marked with gold-brown dots on floor of tube, 18–26 mm long, tube ampliate, to 7–12 mm wide at throat (pressed), lobes 5(–7), oblong to reniform, reflexed-spreading, 8–10 mm long, 6–9 mm wide, emarginate, sparsely pilose on floor of tube, more densely pilose at throat with straight trichomes 0.5–2 mm long, lower lobes pilose and ciliate, upper lobes ciliate only, corolla glabrous throughout outside; stamens (3–)4(–5), anther glabrous, posterior filaments 5–11 mm long, anterior filaments 4–7 mm long, glabrous; styles 9–14 mm long, glabrous; ovaries glabrous. Capsules 3.5–4.5 mm long, glabrous.

Leucophyllum frutescens (figs. 1, 7–10) is characterized by its relatively large shrub habit (1–3 m tall), moderately large, obovate, cuneate-based, bicolored, dorsiventral leaves with both mid and major lateral veins raised beneath, and the relatively large, mostly pinkish to lavender (rarely white) corollas.

The species exhibits considerable variation in leaf vestiture over its range. In all instances, vestiture is less well developed on the upper surface than on the lower surface. At one extreme, generally in plants in the northern portion of the range, both upper and lower leaf surfaces are covered with erect, dendritic trichomes generally 0.1–0.3 mm tall on the upper surface and 0.2–0.5(–1.0) mm tall on the lower surface (fig. 8 c–d). On both surfaces the horizontal radii are 0.06–0.15(–0.2) mm long. Upper leaf surfaces may appear grayish-white or greenish when vestiture is diminished through time.

In other plants (fig. 9 a–d) throughout this northern range the upper leaf surface vestiture is somewhat reduced and consists of a mixture of dendritic trichomes, sometimes with the more distal radii shorter than the

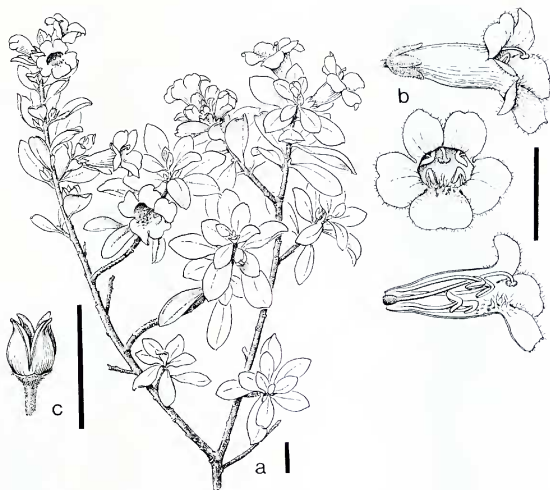


Figure 7. Line drawings of *Leucophyllum frutescens*. a. Stem showing orientation of leaves and flowers. b. Lateral, frontal, cutaway side views of flowers. Note orientation of longer, posterior and shorter, anterior stamens. c. Mature fruit showing characteristic septicidal and loculicidal dehiscence. (From cultivated material in Austin, Texas). Scales = 1 cm.

basal radii on a trichome, and shorter stalked or sessile stellate trichomes (basically reduced dendritic trichomes), or only of stellate trichomes mostly with radii 0.06–0.15(–0.2) mm long. In contrast, the lower leaf surface has a taller, more dense vestiture of dendritic trichomes 0.2–0.5 mm tall again with radii 0.06–0.2 mm long. In these plants upper leaf surfaces often appear green in living plants while the lower surface is distinctly whitish.

The diminution of vestiture continues in the southern portion of the range in Nuevo León and Tamaulipas with upper leaf surface vestiture consisting of often more widely scattered, reduced stellate trichomes sometimes mixed with widely scattered dendritic trichomes but with radii mostly only 0.02–0.06 mm long and occasional radii to 0.1 mm long. Lower leaf surface may consist of dendritic trichomes to 0.2 mm tall with

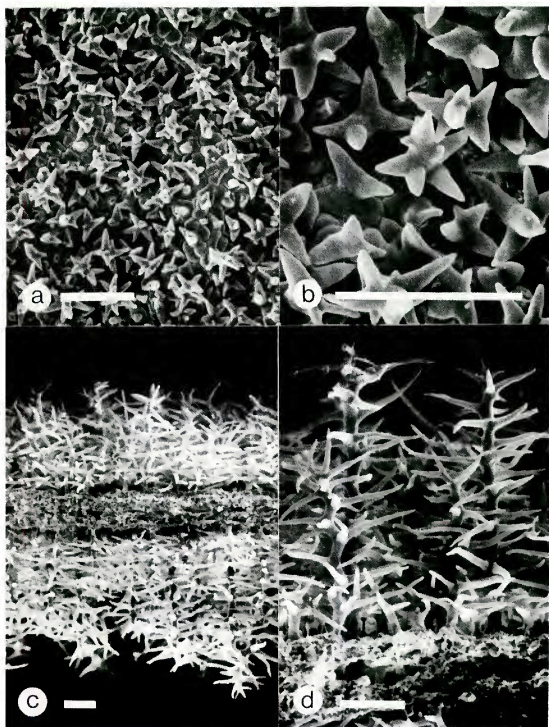


Figure 8. Leaf vestiture of *Lencophyllum langmaniae* and *L. frutescens*. a–b. *L. langmaniae*. Species characterized by uniformly short trichomes with very reduced radii on both leaf surfaces. a. Mature leaf, abaxial surface. b. Trichomes enlarged (*LeSueur* 435). c–d. *L. frutescens*. c. Strongly vestitured leaf showing longer trichomes on abaxial surface. d. Expanded view of lower surface vestiture (shown here downside up). Note each "node" of central axis has 2 or 3 radii. (Compare with fig. 3 b for internal structure). (*Clark et al s.n.*: s. of Sabinas, Coahuila). Scales = 0.1 mm.

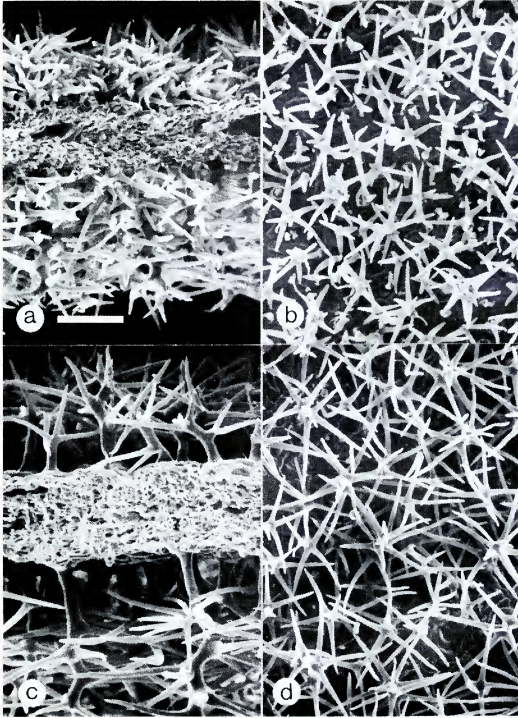


Figure 9. Leaf vestiture of *Lencophyllum frutescens*. a. Cross section of leaf showing shorter vestiture than in fig. 8 c, note also trichomes of lower surface are longer than those of upper surface. b. Surface view of adaxial vestiture. Note moderately spaced trichomes (*Henrickson and Hess* 19052; 20 km sse of Montemorelos, Nuevo León). c. Cross section of leaf showing unbranched base of trichomes and long radii. d. Surface view of adaxial vestiture, note long radii (*Leuts s.n.*; near Amistad Dam, Pecos County, Texas). Scale in a = 0.1 mm; holds for b–d.

radii to 0.2 mm long or only of stellate trichomes with reduced radii similar to those present on the upper surface but still more dense than on the upper surface.

This series culminates in plants with leaves that appear nearly glabrous on the upper surface (fig. 10 a-b, d) but have small, well-spaced, highly reduced stellate and short dendritic trichomes to 0.05 mm tall with radii to 0.02 mm long on the upper surface, and to 0.07 mm tall with radii to 0.04 mm long on the lower surface (fig. 10 c, e). As the branched trichomes are reduced in density, the underlying gland-tipped trichomes, (which are present in leaves of all the species), become more conspicuous.

In Flyr (1970), plants with such reduced vestiture from southern Nuevo León and Tamaulipas were recognized as a distinct variety but the pattern of variation is *clinal* with a general reduction in stature and density of trichome observed in populations from the north into southern Tamaulipas. However, even in these southern populations there is a variation in leaf vestiture: some plants have reduced stellate trichomes with short radii and others have a mixture of stellate and larger dendritic trichomes with longer radii similar to those found in northern populations. Also, occasional plants from Texas such as *McKinney* 039 (LL) from native habitats in Austin (fig. 10 d, e) and *Johnston* 53257.6 (TEX) from Star County have leaf vestiture comparable to that of populations in Tamaulipas and Nuevo León. The only effective way to separate these northern and southern population series would be on the basis of upper leaf surface trichome size with the northern populations having radii mostly 0.06–0.15(–0.2) mm long, those in the southern populations having shorter radii mostly 0.02–0.06 mm long.

Although the trend of diminished vestiture is generally recognizable, the interpopulational variation, the minute nature of the vestiture differences (effectively observed only with magnifications of 30 power or more), the lack of correlated characteristics, makes recognition of varieties along this clinal variation gradient both arbitrary and difficult. Therefore, no infraspecific taxa are recognized.

From a viewpoint in Texas one tends to consider that the species is typically rather strongly vestitured and that the reduced vestiture in southern populations is a derived feature. But paleobiogeographic considerations tend to support the idea that populations with reduced or diminished vestiture in the south may be relictural from pluvial times and that the taxon has been spreading northward and spilling over into the Chihuahuan Desert with more densely vestitured populations.

On the other hand it is hardly defensible to say that the highly reduced vestiture found in some southern populations (fig. 10 a–c) is pleisomorphic because the vestiture is so obviously reduced from a more dendritic

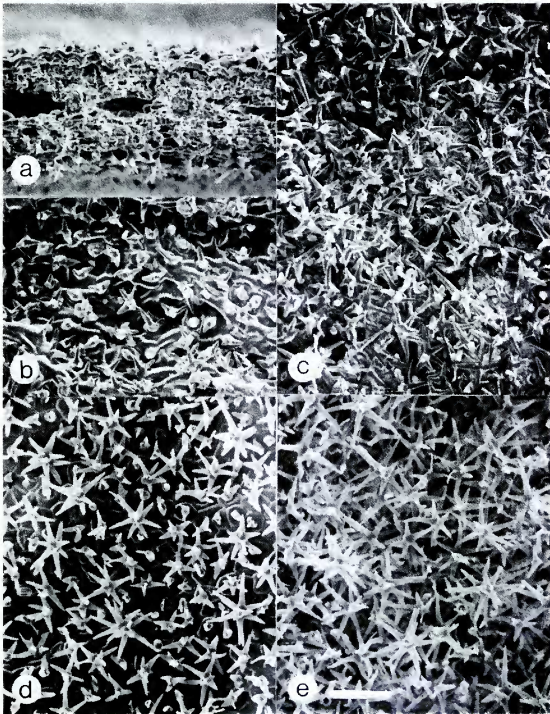


Figure 10. Leaf vestiture of *Leucophyllum frutescens*. a. Cross section of leaf with very reduced vestiture on both surfaces. Compare with fig. 8 c, 9 a, c. Note air lacunae in mesophyll. b. Surface view of adaxial vestiture. c. Surface view of abaxial vestiture, both surfaces are green in color (Graham and Johnston 440: 17 mi S of Victoria, Tamaulipas). d. Surface view of adaxial vestiture. e. Abaxial vestiture of plant from Barton Springs, Austin, Texas, showing similar diminished vestiture (McKinney 039). Scale in e = 0.1 mm; holds for a - d.

type. It is more probable that selection has been occurring in both directions over time.

Leucophyllum frutescens is the widest ranging species in the genus and occurs from Trans-Pecos Texas (Brewster Co.) east through the southern Edwards Plateau to the south Texas plains south through Coahuila, north central Nuevo León to southern Tamaulipas (fig. 11) where it occurs mostly in limestone, calcareous, sandy to clay plains and hills from Chihuahuan Desert to Tamaulipan Thorn Scrub habitats from 5 to 1200 m. The species is commonly cultivated in Texas and over much of the southwestern United States. It is quite cold hardy and can withstand moderate frosts.

2. *LEUCOPHYLLUM langmaniae* Flyr, sp. nov.

A speciebus alliis foliis concoloribus, pubescentiis densis, trichomatibus stellato-dendriticis, radiis 0.01–0.04 mm longis differt.

Erect, alternately-branched shrubs 0.6–2.5 m tall; young stems closely, sometimes irregularly tomentose-canescant with dendritic trichomes 0.04–0.2 mm long, 0.04–0.1 mm wide with blunt, short radii 0.2–0.05 mm long, tardily glabrate; older stems light brown; internodes 1–7 mm long. Leaves alternate, crowded near tips of branches, oblanceolate to spatulate-obovate, 10–8 mm long, 4–9 wide, obtuse, rounded, rarely acute, usually bluntly apiculate to retuse at tip, narrowly cuneate at base, obscurely petiolate, greenish, concolorous, both faces with fairly dense, reduced stellate to stellate-dendritic trichomes 0.03–0.1 mm long and wide, radii very short, sometimes scarcely developed 0.01–0.04 mm long, mixed with scattered glands, trichomes more dense along raised midvein beneath and on petioles. Flowers on slender pedicels 3–8 mm long, calyces 3.5–4.5 mm long, lobes linear-lanceolate to obovate, 3–4 mm long, 1–1.2 mm wide, greenish, closely vestitured as leaves, slightly less than pedicels, greenish, sparsely pilose inside except near tip; corollas lavender-blue, with yellowish dots in floor of tube, 12–26 mm long, tube ampliate to 4–9 mm wide at throat (pressed), lobes obovate, reniform, 4–8(-10) mm long, lower medial lobe emarginate, 5–12.5 mm long, others slightly smaller, all undulate at margin, tube moderately pilose inside with tangled trichomes 1–2 mm long, pilose with shorter hairs at base of lobes near throat, otherwise glabrous, not ciliate, corollas glabrous outside; stamens 4, anthers glabrous, posterior filaments 5–10 mm long, anterior filaments 3–7.5 mm long, glabrous; style 5.6–10.5 mm long, sparsely pilose; ovary sparsely pilose. Capsules 4.5–5 mm long, 3–3.5 mm wide, pilose at tip.

TYPE: MÉXICO. NUEVO LEÓN: hills near Monterrey, 1700 ft, 31 Aug 1903, C. G. Pringle 11656. (HOLOTYPE: SMU!; ISOTYPES: F!, GH!, LL!, MEXU (2 sheets)!, MICH!, PH!, US!).

Additional collections: MÉXICO. NUEVO LEÓN: Obisepado near Monterrey, Feb 1909, *Abluis. n.* (PH); Huasteca Canyon near Monterrey, Aug 1938, *LeSueur* 435 (TEX); 17.2 mi w of Santa Catarina, 3420 ft, 8 Aug 1959, *Youngpeter and Cohn* 62 (MICH) and 9 Aug 1959, *Youngpeter and Cohn* 80 (ENCB, MICH); ca 1 mi from entrance of Huasteca Canyon, 2 Aug 1972, *McGill, Brown, and Pinkava* 9734. (ASU, ENCB), Huasteca Canyon, 0.1 mi below Pozo No. 17, ca 850 m, 12 Aug 1983, *Prigge and Michener* 5311 (RSA, TEX).

Leucophyllum langmaniae is characterized by its oblanceolate, greenish, isolateral leaves covered with a close vestiture of closely-spaced, stellate-dendritic trichomes with very short radii 0.01–0.04 mm long (fig. 8 a, b). In its uniformly short leaf vestiture it differs from all other species in the genus though a similar vestiture occurs on the upper leaf surfaces of some *L. frutescens* from Nuevo León and Tamaulipas, however, in the latter species, leaves are bicolored, with dorsiventral structure and the lower leaf surfaces have denser dendritic trichomes. This similarity in vestiture caused Flyr (1970) to consider relationships with *L. frutescens*. Relationships appear to lie with *L. laevigatum* var. *laevigatum*, which also has greenish leaves equally vestitured on both sides, but with fewer, larger trichomes. In both *L. langmaniae* and *L. laevigatum* var. *laevigatum* newly formed leaves are also green, i.e., the leaves are not covered by a dense layer of trichomes that eventually fall away giving rise to a more open vestiture. They differ, however, in a number of floral features. Their similarity may be entirely due to their shared reduction in vestiture. *Leucophyllum langmaniae* appears to be restricted to the canyons of the Sierra Madre Occidental in Nuevo León between Monterrey and Saltillo (fig. 18); an area of considerable endemism.

The new species is named for Ida K. Langman, author of the monumental guide to the literature of the flowering plants of Mexico.

3. *LEUCOPHYLLUM MINUS* A. Gray in Torrey, Bot. Boundary Surv. 115. 1859. TYPE: TEXAS. PECOS CO.: rocky hills of the Pecos, 4 June 1851, *Wright* 1481 (field number 345) (lectotype: here designated GH!; isotypes: GH!, MO!, NY!).

Leucophyllum minus A. Gray forma *argenteus* Pennell, Proc. Acad. Nat. Sci. Philadelphia 92:295. 1940 [8 Apr 1941]. TYPE: TEXAS. BREWSTER CO.: Persimmon Gap area, 21 Aug 1939, *O.E. Sperry* 1518 (HOLOTYPE: PH!; ISOTYPE: TAES!).

Intricately, alternately-, divaricately-branched shrubs 2–8(-15) dm tall, often rather thorny due to persistence of young dead branches; young stems closely canescent-tomentose with appressed stellate trichomes 0.1–0.2 mm in diameter with rather thick, tapering radii, these tardily glabrescent; older stems reddish-brown to light, rarely dark, gray: internodes 0.5–10 mm long. Leaves alternate, crowded in axillary fascicles or on compressed lateral shoots, oblanceolate or spatulate, to obovate-orbicular, typically small, (2-)3–10(-16) mm long, 1.8–5(-10) mm wide, obtuse to acute, often apiculate at tip, gradually cuneate (sometimes in small or broader leaves abruptly cuneate) to a petiole (0.5-)1–3(-4) mm

long, both surfaces equally silvery-gray, uniformly canescent-tomentose with short dendritic to "stellate" trichomes 0.1–0.2 mm in diameter with radii often appearing to originate from a gland-like umbo, radii broad, tapering, thick- or thin-walled, variously twisted, 0.05–0.1 mm long, occasionally some marginal trichomes more dendritic, midrib slightly raised beneath. Flowers on slender tomentose pedicels 1–3(-5) mm long; calyces 2.8–4.5 mm long, lobes oblong, oblong-lanceolate, (2.2-)3–4.4 mm long, 1–4(-1.9) mm wide, acute, strongly canescent-tomentose as stem outside, glabrous, sparsely glandular inside except at tip; corollas light purple, lavender, rarely pink, white, with white patch marked with yellow-brown dots in floor of throat, 12–18(-24) mm long, tube rather abruptly ampliate 1–3 mm above base, to 6–7 mm wide at throat (pressed), slightly compressed, lobes subequal, orbicular-reniform, obovate, reflexed, 3–7.5 mm long and wide, often emarginate, sparsely pilose in tube with tangled hairs to 2 mm long, more pilose in throat, lobes mostly glabrous to sparsely pilose, distinctly ciliate with hairs 0.2–0.5 mm long, corolla glabrous outside; stamens 4, anthers with short hairs at tip, posterior filaments 5–11.5 mm long, anterior filaments 3–8.5 mm long, glabrous to pilose; style (6-)8–12 mm long, glabrous to sparsely pilose. Capsule usually glabrous, rarely pilose, 4–5 mm long, 2.3–3 mm wide. Chromosome number $n = 16$.

Leucophyllum minus (figs. 15 c, 13 e, f) is characterized by its low, intricately-branched habit with many old stems persisting as thorns, by its small, concolorous, silver-gray leaves crowded on short, lateral shoots and particularly by its distinctive "stellate" vestiture with thick, tapering, broad-based, but thin-walled radii extending from a central stalk (fig. 14 e, f) best seen under 30 X magnification. The vestiture has been described best by Johnston (1941:120): "in *L. minus* the indument is very dense and close and almost suggests a coating of aluminum paint. The very numerous small white trichomes are flat and stellate. The primary axis of the trichomes is extremely shortened and its top appears as a small dot or knob at the center of the radially arranged arms." Actually, the trichomes are not stellate but compressed-dendritic with radii extending from several levels but typically with one series of radii at the top. The terminal, sometimes darkened, trichome tip is not always conspicuous. In young leaves scattered marginal trichomes are clearly dendritic but they weather away and shorten with age. Corollas are typically light purple, usually small, and the lobes are distinctly ciliate.

Leucophyllum minus may occur sympatrically with *L. frutescens* and *L. candidum* in Trans-Pecos Texas and adjacent México (figs. 11, 17, 18). Fly

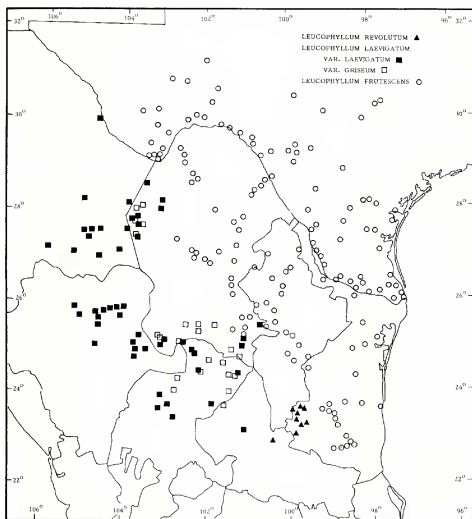


Figure 11. Distribution of *Leucophyllum revolutum*, *L. laevigatum* var. *laevigatum*, *L. laevigatum* var. *griseum*, and *L. frutescens* in Texas and northern México.

(1970) presented evidence of hybridization between *L. minus* and *L. frutescens* in a population in Big Bend National Park.

Leucophyllum minus occurs in rocky limestone to igneous-rock hills, plains, and canyons in *Larrea*. Mixed Desert Scrub, Izotal, and Chaparral in the Chihuahuan Desert region from southeastern New Mexico through Trans-Pecos Texas into northeastern Chihuahua and Coahuila (fig. 18) from 700 to 1700 m.

4. *LEUCOPHYLLUM LAEVIGATUM* Standley

Erect to strongly, alternately-branched shrubs (3-5 – 15(-20) dm tall, stems erect or not, sometimes thorny from persistence of old stems; young stems closely tomentose-canescens with irregular stellate and dendritic

trichomes 0.1–0.2 mm high, radii very short, tapering, 0.02–0.1 mm long, vestiture weathering in time, tardily glabrate; old stems with dark gray to black bark; internodes 1–8(-11) mm long. Leaves alternate, borne on erect long shoots or sometimes in compressed axillary clusters, oblanceolate, obovate (3-)5–18(-27) mm long, (1.3-)3–8(-10) mm wide, obtuse, rounded to truncate, often bluntly apiculate to emarginate at tip, narrowly cuneate to a petiole 1–3.5 mm long as base, at margins entire or variously folded, greenish to canescent-tomentose when young, sparsely to densely vestitured equally on each surface with low stellate to dendritic trichomes 0.1–0.3 mm high, 0.1–0.2(-0.8) mm in diameter with tapering, thin-walled radii 0.02–0.15(-0.2, rarely to 0.5) mm long, but more concentrated along midveins, often gradually glabrate and scattered with interlying glands visible on each surface in mature leaves, mature leaves then green (drying dark brown) but petioles vestitured as stems. Flowers with pedicels (1-)2–5(-9) mm long, vestitured as stems; calyces 2–5 mm long, lobes linear-lanceolate, (1.5-)2.5–4 mm long, to 5.2 mm long in fruit, 0.6–1.2 mm wide at base, acute, sparsely to moderately vestitured with stellate to dendritic trichomes, often with very short radii, with underlying glands often visible, glabrous to glandular inside; corollas lavender-purple, violet, light lavender-violet, rarely blue, white, or purple with whitish patch marked with yellow-brown spots on floor of tube, (10-)14–20(-28) mm long, tube gradually ampliate, slightly compressed, lobes subequal, broadly obovate-orbicular, 4–6.5(-11) mm long and wide, emarginate; tube and throat with tangled hairs 0.5–2 mm long, lobes strongly ciliate, often pilose with shorter trichomes 0.2–0.7 mm long at least on lower lobes inside, corolla glabrous to sparsely stellate, rarely with stipitate glands outside; stamens 4, anthers glabrous or pilose below; styles 4–10 mm long, mostly glabrous to sparsely pilose below; ovaries glabrous or pilose at tip. Capsules oblong in outline, 4–7 mm long, 2.5–3.7 mm wide, glabrous or pilose at tip.

Leucophyllum laevigatum (fig.s 12, 13, 14) is characterized by its small shrub habit with either erect, straight stems or of a more gnarled habit with some old stems persisting as naked thorns, by its alternate, often fasciculate, concolorous, obovate-oblanceolate, cuneate-based, typically green or grayish leaves with a vestiture of open or crowded stellate or mixed stellate-dendritic trichomes 0.1–0.3(-0.8) mm in diameter. Flowers have lavender to purple-violet or blue corollas 10–24 mm long with a yellow-to brownish-spotted whitish patch on the bottom of the throat. Corolla lobes are distinctly ciliate and calyx lobes are linear, usually sparsely vestitured. Two varieties are recognized, separable by the following key:

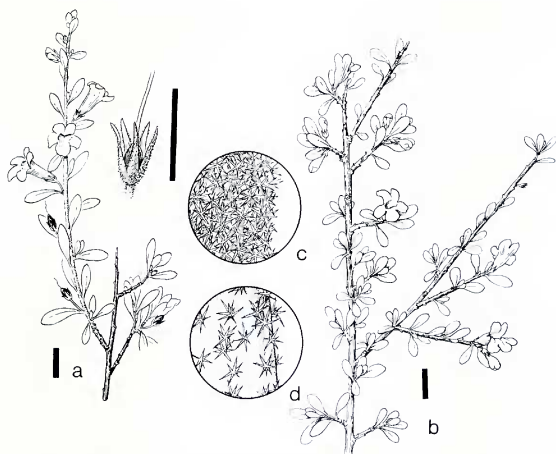


Figure 12. Line drawings of *Leucophyllum laevigatum*. a. *L. laevigatum* var. *laevigatum* stem with characteristic scattered leaves and (in this specimen) large flowers. Note long pedicels, enlarged immature fruit and calyx (upper right) (Chiang, Wendt and Johnston 9041). b–d. *L. laevigatum* var. *griseum*. Stem with characteristic thorny branches, more crowded, smaller leaves. Circular inserts indicate variation of vestiture in young, grayish leaves (c) and mature, more green leaves (d). Scales = 1 cm; c, d circles measure ± 1 mm in diameter.

- A. Young and older leaves both green, thichomes in both typically well-spaced, not or slightly overlapping, radii short, 0.02–0.07(–0.15) rarely to 0.3 mm long; leaves typically (5–)10–18(–27) mm long, borne along erect stems; stems seldom persisting as thorns. . . 4a. *L. laevigatum* var. *laevigatum*
- AA. Young leaves gray, canescent-tomentose with crowded trichomes, mature leaves either gray, with a dense mat of trichomes with radii 0.03–0.16 mm long, or more green with trichome radii overlapping, 0.1–0.5 mm long; leaves 3–10(–15) mm long, crowded into fascicles; plants often thorny with old leafless stems persisting as thorns. . . 4b. *L. laevigatum* var. *griseum*

4a. *LEUCOPHYLLUM LAEVIGATUM* Standley var. *LAEVIGATUM*, Contr. U.S. Natl. Herb. 23:1305. 1924. TYPE: MEXICO. Durango: between Ramos and Inde, 11–14 Aug 1898, E. W. Nelson 4689 (HOLOTYPE: US!; ISOTYPES: GH!, K!, PH!).
Leucophyllum laevigatum Standley var. *coahuilensis* Kiger, *Rhodora* 74:347. 1972. TYPE:

MÉXICO. COAHUILA: Caneros Pass area, along México Hwy 54, about 23 mi S of Saltillo, 5 Aug 1971, J. L. Reveal, W. H. Hess, and R. W. Kiger 2617 (HOLOTYPE: US!; ISOTYPES: LL!, and elsewhere).

Erect-stemmed shrubs 5–15(-20) dm tall, seldom with old stems persisting as thorns. Leaves alternate, sometimes also in axillary fascicles, (5-)10–18(-27) mm long, (2.5-)4–8(-10) mm wide, green when young and at maturity, trichomes stellate to dendritic-stellate, radii 0.2–0.8 (-0.15, rarely to 0.3) mm long, trichomes mostly well-spaced on mature leaves except along midvein; pedicels 3–9 mm long; ovary and style mostly glabrous.

In *Leucophyllum laevigatum* var. *laevigatum* (fig. 12 a) both young and mature leaves are green with moderately- to well-spaced, stellate to stellate-dendritic trichomes with short, rather thickish, tapering, translucent radii 0.2–0.8(-1.5) mm long (fig. 13 a–d). Similar but much more crowded trichomes cover young stems and this denser vestiture extends onto petioles and often along the midribs of both leaf surfaces. This vestiture pattern is found throughout the range of the taxon, except in eastern Durango and west-central Coahuila where plants tend to have some leaves with larger trichomes with radii to 0.3 mm long (fig. 13 a, b). The variety also tends to have a more erect habit with stems bearing alternate leaves.

Corolla color varies and Kiger (1972) described a new variety from the Caneros Pass area in southeastern Coahuila with strong blue corollas.

This variety occurs in limestone, caliche hillsides and alluvial fans in the Chihuahuan Desert from southeastern Chihuahua, western and southeastern Coahuila, and eastern Durango to Zacatecas, and San Luis Potosí (fig. 11) from *Larrea*, Mixed Desert Scrub to Izotal zones from 1200 to 2200 m.

4b. *LEUCOPHYLLUM LAEVIGATUM* Standley var. *griseum* (I. M. Johnston)

Henrickson comb. et stat. nov. *Leucophyllum griseum* I. M. Johnston, J. Arnold. Arbor. 22:119. 1941. TYPE: MÉXICO. COAHUILA: foothills of the Sierra Planchada, 6 mi N of Esmaralda, 16 Aug 1940, I. M. Johnston and C. H. Mueller 341 (HOLOTYPE: GH!; ISOTYPE: LL!).

Leucophyllum virens I. M. Johnston, J. Arnold Arbor. 21:253. 1940. TYPE: MÉXICO.

DURANGO: near La Loma valley of the Rio Nazas, 4900 ft, 22 Aug 1939, F. Sbrève 9191 (HOLOTYPE: GH!)

Low, rounded shrubs 3–10(-18) dm tall; typically with old naked branches persisting as thorns. Leaves alternate and crowded in axillary fascicles in distal 2–5(-12) cm of branches, 3–10(-15) mm long, 1.3–5(-7) mm wide; young leaves gray, densely covered with a close vestiture of stellate, stellate-dendritic to dendritic trichomes, older leaves gray, densely vestitured or green with a sparse vestiture, trichome radii

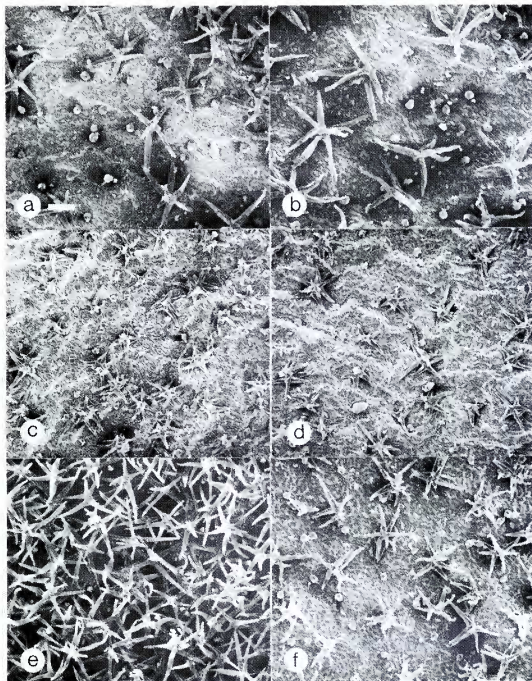


Figure 13. Leaf vestiture of *Leucophyllum laevigatum*. a-b. *L. laevigatum* var. *laevigatum*. In typical variety, both young (a) and old (b) leaves are green, with scattered, well-spaced trichomes. Note sessile glands (adaxial surfaces) (*Flyr 672a*: near Pedricena, Durango). c-d. *Laevigatum* var. *laevigatum*. Phase with smaller well-spaced trichomes equally distributed in young (c) and mature (d) leaves (abaxial surfaces) (*Correll and Johnston 20238*: 11 mi E La Zarca, N of Durango). e-f. *L. laevigatum* var. *griseum*. In this variety young leaves are gray with dense vestiture (e), mature leaves may be gray or green (f) with sparse vestiture, (abaxial surface) (*Johnston and Mueller 341*: isotype of *L. griseum* from N of Esmaralda, central Coahuila). Scale in a = 0.1 mm, holds for b-f.

(0.03-)0.1-0.16(-0.3, rarely to 0.5) mm long; peduncles 1.5-5 mm long; ovary and styles mostly pilose.

Leucophyllum laevigatum var. *griseum* occurs in west-central and southern Coahuila and adjacent northern Zacatecas and San Luis Potosí (fig. 11). In several areas it is sympatric and appears to intergrade with *L. l.* var. *laevigatum*. In Flyr (1970) *L. laevigatum* and *L. griseum* were recognized as distinct species distinguished in the key by habit with *L. griseum* having persistent, leafless, short, lateral branches giving the plants a thorny appearance while *L. laevigatum* characteristically had longer, leafy shoots and specimens lacked such short, lateral branches unless the plants had been browsed (Flyr 1970). While such habit differences can be recognized in most specimens, they are not consistent and certainly can be influenced by environmental conditions.

Vestiture differences tend to correlate with habit. In the more openly-branched variety *laevigatum* both young and mature leaves are green, with an open, typically non-overlapping vestiture of trichomes typically with short radii. In the more tightly-branched variety *griseum* with shorter, more crowded leaves, the young leaves are gray with a dense, low vestiture and mature leaves may either retain this dense gray vestiture or the vestiture may thin; the mature leaves are then green. In many southern Coahuila, Zacatecas, and San Luis Potosí populations of variety *griseum* both young and mature leaves are gray, covered with a dense to moderately dense vestiture of stellate or a mixture of stellate and short-dendritic trichomes with short radii 0.02-0.08(-0.15) mm long, basically with trichomes with short radii similar to those of variety *laevigatum* but very crowded.

In specimens of variety *griseum* from west-central Coahuila (including the type of *L. griseum*), young leaves tend to be gray, densely vestitured with stellate and dendritic trichomes, however, as the leaves mature, dendritic trichomes with short radii tend to fall away and the remaining stellate, stellate-dendritic trichomes are more dispersed, though typically with overlapping radii (fig. 13 e, f). They also tend to have longer radii, 0.1-0.2 mm long, similar to the longer-trichome radii found on leaves of variety *laevigatum* in that region. In some specimens trichomes on young leaves have long radii at the base and short radii in distal portions and as leaves mature the distal portions of the trichomes fall away leaving the larger basal radii. A similar pattern is seen in some specimens of variety *griseum* in northern Zacatecas.

This trend reaches its extreme in southwestern Coahuila and adjacent Durango, where in some specimens, young leaves are gray with a dense, close vestiture of trichomes with short radii (fig. 14 a) and older leaves are greenish, with moderately dense, typically overlapping, large trichomes



Figure 14. Leaf vestiture of *Lencophyllum laevigatum* var. *griseum* and *L. minus*. a–b. *L. laevigatum* var. *griseum*. Vestiture similar to that of type of *L. virescens*; young leaf has dense, short vestiture (a); mature leaves have very sparse vestiture with radii to 0.4 mm long (b), (abaxial surfaces) (Chiang, Wendt and Johnston 9550; near Sierra Jimulco, Coahuila). c–d. *L. laevigatum* var. *griseum*. In S Coahuila, Zacatecas, vestiture of both young (c) and mature (d) leaves is dense and both young and mature leaves are gray (adaxial surfaces) (Sanford, Retherford and Northcraft 157; S of Parras, Coahuila). e–f. *L. minus*. Both young and old leaves have dense vestiture of “stellate”, actually short dendritic trichomes. e. Mature leaf, abaxial surface (McGill and Keil 7626). f. Enlarged view showing broad, flat radii. Base at radii at trichome tip often darken giving appearance of a terminal gland (Engard and Gentry 605). Scale in a = 0.1 mm, holds for a–e, f = 0.1 mm.

with radii 0.13–0.5 mm long (fig. 14 b). In some specimens trichome radii vary among adjacent leaves on a stem; some leaves have trichome radii 0.13–0.2 mm long, others have radii 0.2–0.5 mm long, indicating that trichome radii development may be influenced by environmental conditions.

A specimen with this type of long-rayed trichomes similar to that shown in fig. 14 b was designated the type of *L. virescens* by I. M. Johnston (1940), who emphasized the short trichome radii on young leaves in contrast to the long radii on trichomes of old leaves. However, the specimen appears to be completely referable to variety *griseum* and differs only in its very long trichome radii. Additional specimens bridge the gap between this specimen and typical *griseum*. Flyr (1970) considered *L. virescens* to be a hybrid between *L. laevigatum* and *L. candidum* because specimens referable to these two taxa were the only plants found during two searches at the type locality of *L. virescens*. The occurrence of trichomes with long-basal radii and short distal radii and others with only short radii is reminiscent of those of *L. candidum* but the specimen exhibits no other features of *L. candidum*.

Whether *L. l.* var. *griseum* merely represents a more xeromorphic derivative of *L. l.* var. *laevigatum*, i.e., with a reduced, more thorny habit, more strongly vestitured leaves, or presents intergradation with *L. candidum*, or other more densely vestitured species, is not known. Specimens available indicate a continuum of variation between the two varieties. The line between the two taxa must be drawn arbitrarily. Distinction on the basis of habit (sensu Flyr, 1970) versus vestiture (emphasized here) gives a slightly different assignment of specimens that have long, erect stems (as in variety *laevigatum*) but dense vestiture on young leaves (as in variety *griseum*).

The younger epithet *griseum* (Johnston 1941) is recognized at the varietal level over the older *virescens* (1940) because the type of *griseum* is more representative of the taxon and *griseum* has been more widely used than *virescens*.

Leucophyllum l. var. *griseum* grows on limestone and calcareous hillsides from Larrea- to Yucca-dominated zones to chaparral from 1400 to 2400 m (fig. 14).

5. *LEUCOPHYLLUM CANDIDUM* I. M. Johnston, J. Arnold Arbor. 22:120. 1941 [15 Jan 1941]. TYPE: MÉXICO. COAHUILA: between Carrizo and Carricito on (gypsaceous?) ridge, 11 Aug 1940, I. M. Johnston and C. H. Mueller 160 (HOLOTYPE: GH!; ISOTYPE: LL!).

Leucophyllum violaceum Pennell, Proc. Acad. Nat. Sci. Philadelphia 92:295. 1940 [8 Apr 1941]. TYPE: TEXAS. BREWSTER CO.: frequent on flats from Lone Mountain to

Nugent Mt., Chisos Mt. area, 2 Aug. 1937, B. H. Warnock 1124 (HOLOTYPE: US!; ISOTYPES: GH!, PH!, SRSC, TAES!, TEX!).

Compact, divaricately, alternately-branched, rounded to erect shrubs 3 – 10(-15) dm tall; young stems densely, unevenly tomentose with spreading dendritic trichomes, the longer 0.2 – 0.7 mm long, 0.15 – 0.3 mm in diameter, these eventually weathering to a more uniform stature and eventually glabrate; older stems red-brown to light or dark gray. Leaves alternate to subopposite, often opposite near tip of stem, often with reduced

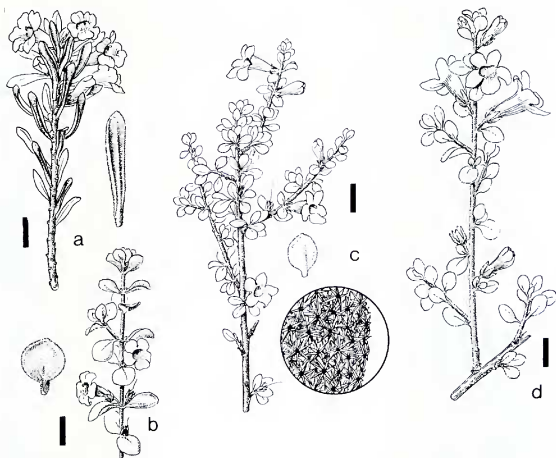


Figure 15. Line drawings of *Leucophyllum* species. a. *L. revolutum*. Stem showing characteristic orientation of leaves, flowers. Note swollen residual leaf bases at nodes. Leaf in abaxial view shown to right (Johnston, Wendt and Chung 11181). b. *L. zygophyllum*. Stem, note opposite, conduplicate-folded leaves and flowers. Leaf in adaxial view at left (Correll and Johnston 19860). c. *L. minus*. Stem showing characteristic thorny habit, small, crowded leaves, flowers. Circular insert represents vestiture consisting of low, dense "stellate" trichomes that tend to develop darkened dots at tips (Chiang, Wendt and Johnston 7703). d. *L. candidum*. Stem, note leaves and large flowers. The species is characterized by mostly alternate leaves and dendritic trichomes (Warnock 257). Scale = 1 cm, separate leaves shown 2 x larger. Circle with vestiture measures ± 1 mm in diameter.

leaves in axillary shoots, mostly broadly obovate to obovate-orbicular, reniform, occasionally some ovate, 6–10(-16) mm long, 3.5–7(-10) mm wide, rounded, obtuse, occasionally acute, often bluntly apiculate or appearing emarginate by recurving of midrib tip, rounded, abruptly, occasionally gradually, cuneate at base above a petiole 1–3(-6) mm long, at margins entire, rarely revolute, initially densely, equally gray-tomentose (often turning tan in herbarium specimens) on both faces with uneven tapering-cylindrical dendritic trichomes 0.15–0.6 mm long, 0.1–0.3 mm wide, with slender, tapering radii 0.05–0.2 mm long, longer trichomes somewhat weathering in time and vestiture more uniform in height and exposing longer basal radii 0.1–0.3 mm long. Flowers on densely tomentose pedicels 1–4.5 mm long; calyces 4–7(-9) mm long, lobes oblong, oblong-lanceolate, 2.5–5(-6) mm long, 0.7–1.7(-2.5) mm wide, densely tomentose with elongate cylindrical dendritic hairs as on young stems outside, glabrous, gland-dotted except at tip inside; corollas dark to light violet-purple, with white patch marked with orange to yellow-brown dots on floor of tube, (10-)12–22(-25) mm long, tube ampliate, somewhat compressed, 5–8 mm wide at throat (pressed), lobes subequal, suborbicular, emarginate, 3–7(-11) mm long and wide, strongly to moderately long-pilose inside lower tube with tangled hairs 0.5–2 mm long, pilose with shorter, often blue-tipped, wavy hairs 0.2–0.7 mm long inside and on margins of lobes, corollas loosely stellate to glabrous outside; stamens 4, anthers with stellate tuft at tip, posterior filaments 5–10.5 mm long, anterior filaments 5–7 mm long, glabrous to pilose; styles 6–9.5 mm long, sparsely pilose in lower half to glabrous; ovaries pilose above. Capsules 4–5 mm long, pilose at tip.

Leucophyllum candidum (figs. 15 d, 16) is characterized by its mostly low, densely-branched habit, by its mostly alternate or partially opposite, crowded, often small, broadly obovate, suborbicular, non-conducuplicately folded leaves with a well-developed layer of dendritic trichomes 0.2–0.5 mm thick on both faces with radii 0.05–0.25 mm in length. It can be distinguished from the closely related *L. zygophyllum* because the latter more consistently has opposite, conducuplicately folded leaves with a close vestiture. In contrast leaves of *L. candidum* are flatish or variously undulate-cripsed with a thicker vestiture.

Trichomes of young stems and leaves are dendritic, rather cylindrical, 0.2–0.6 mm tall with slender, wavy radii 0.1–0.2(-0.3) mm long at the base but only 0.05–0.1(-0.2) mm long in the upper two-thirds. In young leaves and stems, vestiture is quite thick and uneven with scattered, longer, cylindrical hairs apparent particularly on the stems and lower leaf margins.



Figure 16. Leaf vestiture of *Lencophyllum candidum*. a – b. Young stems and leaves have dense vestiture; scattered trichomes have long, narrow, terminal portions and these often fall away in time to expose basal, longer radii (Henrickson 12088b). c. In this specimen, terminal portions of trichomes were much reduced (aborted); note longer basal trichome radii (Chiang, Wendt and Johnston 12098). d. Cross section of leaf showing trichomes of both faces. Note also air lacunae in leaf mesophyll and lack of radii on basal portion of trichomes (Henrickson 6093). Scales = 0.1 mm.

However, as the hairs weather away, the longer basal radii are exposed resulting in an apparent change in vestiture to one with longer radii (fig. 16).

There exists a rather perplexing variation pattern within the species. Plants from eastern Durango and central Chihuahua, and some from

Brewster Co., Texas, have corollas, 17–27 mm long versus 9–15(–16) mm for other specimens. These longer-flowered populations also tend to have, on the average, longer trichome radii (0.1–0.2 mm long for upper radii and 0.1–0.3 mm long for the lower radii) as compared to more eastern populations with upper radii 0.05–0.1(0.15) mm long and lower radii 0.1–0.25 mm long. Many specimens from Brewster Co., Texas, also have longer calyces, 6.5–9 mm versus 4–6 mm long in Durango-Chihuahua collections. Because of their geographical separation it is tempting to recognize these western populations as distinct at least at the varietal rank, and there are many botanists who need less than that to describe a new taxon. However, field observations in the Big Bend area of Texas show that these large-flowered plants are probably hybrids with *L. frutescens* rather than a distinct taxon. Similar long-flowered populations occur in *L. minus* in the same area and occur scattered throughout the range of *L. laevigatum*. Field observations indicate that some genetically controlled variation in total corolla length is the norm for certain species of *Leucophyllum*. Though the occurrence of populations with large corollas in Durango and central Chihuahua may represent a monophyletic group, the occurrence of specimens with long corollas in the Big Bend area where short corollas are the norm probably represents an independent evolution of the trait and makes any taxon based on corolla length polyphyletic. Collections of these eastern Durango populations were annotated *L. violaceum* by Flyr but reduced to synonymy under *L. candidum* in Flyr (1970). *Leucophyllum violaceum* is a direct synonym of *L. candidum* and represents the short-flowered populations.

Over its range *L. candidum* occurs sympatrically with *L. frutescens*, *L. laevigatum* var. *laevigatum*, and *L. l.* var. *griseum* (Flyr 1970; Johnston 1941). It ranges from Big Bend area of Trans-Pecos Texas south to central Chihuahua (at La Bufa near Batopilas) and south through Coahuila to eastern Durango and northern Zacatecas (fig. 17) mostly on limestone hillsides, plains in *Larrea*, Mixed Desert Scrub to Izotal vegetations from 800 to 1500 m.

6. *LEUCOPHYLLUM ZYGOPHYLLUM* I. M. Johnston, J. Arnold Arbor. 21:263. 1940. TYPE: MEXICO, NUEVO LEÓN: Puerto de Pastores, SE of Galeana, 2 Aug 1934, C. H. and M. T. Mueller 1299 (HOLOTYPE: A!; ISOTYPES: GHI, MICH!, TEX!).

Erect, oppositely- to alternately-branches shrubs 2–10(–20) dm tall; young stems densely, unevenly silver-gray tomentose with longer conical, dentric trichomes 0.1–0.5 mm long, 0.1–0.2 mm in diameter with short tapering radii, vestiture weathering in time, tardily glabrate; older

stems with gray to tan bark; internodes (2-)5–10(-15) mm long. Leaves opposite, occasionally subopposite, broadly ovate to broadly obovate to orbicular, 4–13(-17) mm long, 3.5–11(-13) mm wide, rounded, bluntly apiculate at tip, rounded to broadly cuneate to a 1–1.5 mm long petiole at base, mostly conduplicately folded, often strongly reflexed at petiole, thick, silver-gray, equally, irregularly, densely tomentose on both sides, longer dendritic trichomes (0.1-)0.2–0.4 mm long, 0.1–0.2 mm in diameter, radii short, tapering, 0.02–0.1 mm long, trichome axis not straight, longer trichomes often along raised midrib beneath and along margins, these weathering and vestiture more uniform in older leaves. Flowers with tomentose pedicels 1.5–3(-5) mm long; calyces 3.5–5 mm long, lobes oblong-lanceolate, 3–3.5 mm long, 0.7–1.1 mm wide, acute, slightly less strongly vestitured than pedicels with dendritic trichomes to 0.2 mm long, glabrous except for stipitate glands below tip inside; corollas purple to light violet with a white patch with gold-brown dots on floor of tube, 11–15(-17) mm long, tube campanulate-funnelform, to 3–6 mm wide at throat (pressed), lobes obovate to orbicular, subequal, 3–7 mm long and wide, wavy, emarginate, tube and throat with sparse to dense, tangled hairs 0.5–1.5 mm long inside, lower lobes often densely pilose with often violet-tipped hairs 0.2–0.5 mm long, corolla glabrous outside; stamens 4, anthers with short hairs at tip, posterior filaments (4-)5–7 mm long, anterior filaments (4-)5–6 mm long, slightly pilose; styles 5–8 mm long, slightly pilose near base; ovary pilose with branched trichomes. Capsules 3–5 mm long, 2.5–3 mm wide, sparsely vestitured with dendritic hairs near tip, trichomes with long radii, sparsely glandular below.

Leucophyllum zygophyllum (fig. 15 b) is a strongly-branched, rounded shrub characterized by opposite, broadly ovate to orbicular, abruptly cuneate to rounded-based, petiolate leaves that are densely, equally tomentose on both surfaces. Typically the leaves are conduplicately folded along the midrib and may be ascending or more frequently divergent or reflexed beyond the recurring petiole. Leaves are often small, but when larger (as in *F. Medellin Leal* 1557 and *F. Gonzalez* M. 9066, both MEXU), leaves may be alternate, flattened with raised lateral veins and vegetatively approach *L. ambiguum*. These plants also tend to have longer trichomes as in *L. candidum*. Whether these plants came from shaded habitats is not known. Flowers in this species are dark purple to violet with yellow spots in the tube and have a slight lavender odor.

Leucophyllum zygophyllum appears to be most closely related to *L. candidum* differing mainly in the opposite, conduplicately-folded leaves and the closer vestiture. It may occur sympatrically with *L. pruinatum* and *L. revolutum* on

rocky limestone, and caliche, rarely gypseous habitats in mesquite to chaparral, oak-pine forests in southern Nuevo León, southwestern Tamaulipas, and adjacent San Luis Potosí (fig. 17) from 1200 to 2100 m.

7. *LEUCOPHYLLUM REVOLUTUM* Rzedowski, Ciencia 15:94. 1955. TYPE: MÉXICO. SAN LUIS POTOSÍ: E of Nuncz, km 84 on highway from San Luis Potosí to Antiguo Morelos, 18 Nov 1954, *Rzedowski* 5611 (HOLOTYPE: MEXU!; ISOTYPE: SLP!)

Erect, alternately-, rather closely-branched shrubs 5–25 dm tall; young stems densely tomentose with erect, conical, dendritic trichomes 0.05–0.3 mm long, radii tapering, 0.05–0.1 mm long, trichomes tardily glabrate; older stems light gray with corky periderm. Leaves alternate, crowded in terminal 5–15 cm of stems, with internodes 1–2(–5) mm long, ascending, oblanceolate, 10–26 mm long, 2–4(–5) mm wide, obtuse, bluntly apiculate at tip, cuneate to base, at margins entire but distinctly revolute, sometimes inrolled in lower half, bicolored, greenish, closely tomentulose with stellate-dendritic trichomes 0.05–0.1 mm long above, densely white tomentose with dendritic trichomes 0.1–0.3 mm long, 0.1–0.2 mm wide, with slender radii 0.05–0.1 mm long beneath. Flowers with tomentose pedicels 1.5–2.5 mm long; calyces 4.2–5.5 mm long, lobes oblong-ovate, 2.5–3.5 mm long, 1.2–1.4 mm wide, acute to obtuse at tip, densely tomentose with conical, dendritic trichomes 0.1–0.2 mm long outside, more glabrous, glandular inside; corollas violet to purple, with white or whitish-purple patch on floor of throat marked with dark violet spots, yellow at very base, 10–18(–20) mm long, tube ampliate to campanulate, dorsiventrally compressed, to 6–8 mm wide at throat, lobes orbicular-obovate, emarginate, spreading, 4–8 mm long and wide, anterior 3 larger than posterior 2, tube rather densely long pilose with tangled trichomes to 2 mm long inside on floor, lobes glabrous, corolla sparsely glandular-pilose outside; stamens 4, anthers with a tuft of hairs at tip or glabrous, white or suffused with purple, posterior filaments 6–9 mm long, anterior filaments 6–7 mm long, pilose; styles 7–12 mm long, pilose; ovaries pilose at tip. Capsules 4 mm long, 2 mm wide, pilose near tip.

Leucophyllum revolutum (figs. 15, 2 a, b) is a very distinct species readily distinguished by its oblanceolate, distinctly bicolored, revolute to inrolled-margined, ascending leaves that are usually crowded along the distal portions of the stems. The violet corollas are distinctive due to their dark purple spots on the floor of the tube and throat.

The relationship of this species within the genus is uncertain. Its leaves are bicolored as in *L. frutescens* but phenetically it tends to cluster with *L. flyrii*. The species occurs sympatrically with *L. zygodphyllum* and *L. prinosum*

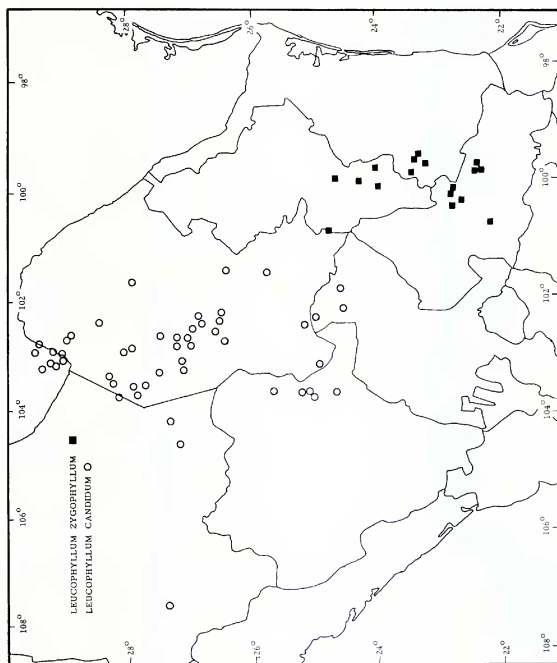


Figure 17. Distribution of *Leucophyllum zygophyllum* and *L. candidum* in southern trans-Pecos Texas and northern México.

on rocky hillsides from *Larrea* scrub to chaparral or submontane scrub in southwestern Tamaulipas near Miquihuana and Bustamente and adjacent northern San Luis Potosí east of El Huizache Junction (fig. 11) over an elevational range of 1600 to 2200 m.

8. *LEUCOPHYLLUM FLYRII* B. L. Turner, Sida 5:54. 1972. TYPE: MÉXICO. SAN LUIS POTOSÍ: 4.4 mi NE of Laguna Seca (Gral. Candido Navarro), 29 Jul 1966, D. Flyr 1113 (HOLOTYPE: TEX!).

Strongly, alternately-branched, rounded shrubs 5–16 dm tall, often rather thorny due to persistence of young dead branches; young stems densely, unevenly, silvery-gray tomentose with dendritic trichomes 0.2–0.4 mm long, 0.2–0.3 in diameter, radii wavy, slender, 0.1–0.2 mm long, trichomes weathering, vestiture more uniform in time, tardily glabrate; older stems with dark gray bark; internodes 2–8 mm long. Leaves alternate, oblanceolate to obovate-spathulate, broadest in distal one-fourth, 10–22(–27) mm long, 4–9(–11) mm wide, obtuse, sub-rounded, bluntly apiculate at tip, tapering to a cuneate base, true petiole not discernible, at margins entire, densely unevenly gray (slightly tan in herbarium specimens) tomentose on both faces with dendritic trichomes 0.1–0.4 mm long, radii wavy, slender, 0.1–0.2 mm long, trichomes diminishing in stature through weathering; midrib raised beneath. Flowers with tomentose pedicels 1–3 mm long; calyces 5–6.5 mm long, lobes lanceolate, 4.5–5.5 mm long, 1.1–1.5 mm wide, acute-attenuate, sparsely beset with dendritic hairs and slender, spreading, stipitate-glandular trichomes 0.1–0.3 mm long, glabrous inside except for stipitate glands; corollas purple to light violet with small dark purple spots throughout lower tube, yellow only at very base, (16–)19–21(–25) mm long, tube broadly ampliate, slightly compressed, to 8 mm wide at throat (pressed), lobes obovate, subequal, 5–7 mm long and wide, emarginate, tube sparsely pilose on floor inside with crinkled hairs 1–2 mm long, lobes nearly glabrous inside, not ciliate, corolla sparsely stipitate glandular outside; stamens 4, anthers glabrous, posterior filaments 8–10.5 mm long, anterior filaments 6–9 mm long, glabrous; styles 10–12 mm long, sparsely pilose near base; ovaries sparsely pilose, stipitate-glandular at tip. Capsules dark brown, 5–6 mm long, 3–4 mm wide, pilose near tip.

Leucophyllum flyrii is distinguished by its somewhat thorny habit, oblanceolate to obovate, cuneate-based leaves that are equally tomentose on both sides with dendritic trichomes with moderately long wavy radii. In addition the calyces, unlike any other species in the genus, have an overstory of slender stipitate glands on the outer surface and are less strongly vestitured than the pedicels. The corollas have broadly ampliate tubes, with dark purple dots to 1 mm wide on the floor of the tube. It is known from a few localities northeast of Ciudad San Luis Potosí in the southernmost margin of the Chihuahuan Desert and in the adjacent Sierra San Pedro (fig. 18) from 1800 to 2200 m.

9. *LEUCOPHYLLUM PRUINOSUM* I. M. Johnston, J. Arnold Arbor. 22:119. 1941. TYPE: MÉXICO. SAN LUIS POTOSÍ: 11 mi S of Marehuala, 10-11 Sep 1938, I. M. Johnston 7569 (HOLOTYPE: GH!).

Strongly, alternately-branched shrubs sometimes somewhat thorny due to persistence of old stems, (3-)8–15(-26) dm tall; young stems loosely tomentose with dendritic trichomes 0.3–0.8 mm long, with long, slender, wavy radii 0.1–0.5 mm long, vestiture tardily glabrescent; old stems with gray to brownish bark. Leaves alternate, orbicular to broadly ovate, rarely broadly elliptical, 8–16(-27) mm long, 6–13(-17) mm wide, rounded, obtuse, often obscurely apiculate at tip, rounded to abruptly cuneate above petiole 1–3.5(-6) mm long at base, at margin entire to crisped-undulate or variously folded, densely but loosely gray tomentose on both faces (sometimes slightly tan in herbarium specimens) with elongate dendritic trichomes 0.4–0.8 mm long with slender, wavy radii 0.1–0.3(-0.5) mm long, trichomes often more dense along raised midvein beneath. Flowers on tomentose pedicels 1.5–3 mm long; calyces 4–6.5 mm long, lobes oblong-lanceolate, 3–5 mm long, 1–1.7 mm wide, acute to attenuate, often unequal, densely tomentose outside and near tip inside as young stems, sparsely to moderately pilose, glandular inside; corollas dark purple to violet with a reddish tinge, with a large white patch with gold dots in floor of tube inside, with grape odor, 8.5–11(-14) mm long, tube broadly campanulate, abruptly expanded above base, (5-)7–9 mm broad at throat (pressed), lobes orbicular, obovate, subequal, 3–5 (-6.5) mm long and wide, sometimes crisped, often emarginate, tube long pilose only in the tube base and lower throat, lobes mostly glabrous, ciliate with shorter hairs, corolla stipitate-glandular outside; stamens 4, anthers pilose at tip, posterior filaments 5–9 mm long, anterior filaments 3–4.5 mm long; styles 5–9(-11) mm long, sparsely pilose; ovaries densely pilose and stipitate-glandular at tip. Capsules 3.5–5 mm long, 2.3–3 mm wide, pilose at tip.

Leucophyllum pruinosa (fig. 19 a) can be distinguished by its distinctive vestiture of large dendritic trichomes with slender radii 0.1–0.5 mm long; the consistently longest trichome radii found in the genus (fig. 20 b), the orbicular to suborbicular, petiolate leaves usually with finely crisped to undulate-folded margins, and the relatively short corollas with the distinctive campanulate tube that abruptly increases in diameter above the base. It is most similar to *L. ultramonticola* as discussed under that species. It differs from *L. ambiguum* in the conspicuous yellow-spotted white patch on the corolla-tube floor. Niezgoda and Tomb (1975) noted this was the only species of *Leucophyllum* with rugulate rather than reticulate pollen sculptur-

ing. Tomb (pers. comm. 1984) noted differences also occur in seed sculpturing. The species can occur sympatrically with *L. revolutum* and *L. zygothymum* but no hybrids have been observed. *Leucophyllum pruinosum* occurs on rocky limestone slopes and alluvial fans in *Larrea* to Mixed Desert Scrub from southern Nuevo León, southwestern Tamaulipas, and eastern San Luis Potosí (fig. 18) from 1000 to 1600 m.

10. *LEUCOPHYLLUM ultramonticola* Flyr sp. nov.

A *L. pruinosum* ovaris et stylis glaberis non pilosis, corollas lobis inferis pilosis non glabris, foliis orbicularibus, distributione in Zacatecas meridio-occidental differt.

Alternately- rather openly-branched, erect shrubs 10–17 dm tall; young stems irregularly, densely gray-tomentose (turning brown in herbarium specimens) with cylindric, dendritic trichomes (0.1–)0.3–0.7 mm long with slender, wavy radii 0.1–0.2 mm long, tardily glabrate, older stems light gray, often remaining as coarse thorns; internodes 1–10 mm long. Leaves alternate, crowded, broadly ovate-orbicular to broadly elliptical, 10–25 mm long, 8–25(–30) mm wide, obtuse to rounded, occasionally retuse or bluntly apiculate at tip, abruptly cuneate-rounded at base above a tapering petiole 2–5 mm long, at margins entire, undulate, densely gray to rather greenish (turning brownish in herbarium specimens), tomentose on both faces with dendritic trichomes (0.1–)0.2–0.4(–0.7) mm long, radii slender, straight or wavy (0.1–)0.2–0.4 mm long, trichomes weathering, becoming more uniform in age, midvein and in larger leaves basal, lateral veins prominent beneath. Flowers with tomentose pedicels 3–3.5 mm long; calyces 5.5–8(–9.2) mm long, lobes oblong to oblanceolate, 4.2–7 mm long, 1.3–2.1 mm wide, obtuse-acute, densely tomentose as stems outside and inside at tip, moderately sericeous-pilose inside, glabrous, sparsely glandular near base inside; corollas purple-violet, with a large yellow patch marked with red-brown spots on tube floor inside, 12–16 mm long, tube broadly campanulate, to 6.5–8.5 mm broad at throat (pressed), lobes obovate, 4–5 mm long and 3.5–4.5 mm wide, truncate to emarginate at tip, undulate, short ciliate, tube with long tangled hairs 1.5–2 mm long on basal floor, lobes pilose with shorter, wavy hairs 0.3–0.5 mm long, to 1.0 mm long near throat; corolla glabrous to very sparsely stipitate-glandular outside with hairs 0.1–0.2 mm long; stamens 4, posterior filaments 8.5–10 mm long, anterior filaments 5–6.5 mm long, glabrous; styles 9–10 mm long, glabrous; ovaries glabrous. Capsules 4.5 mm long, 2.5 mm wide, glabrous except for some stipitate glands near base.

TYPE: MÉXICO, ZACATECAS: San Juan Capistrano, 21 Aug 1897, J. N. Rose 2452 (HOLOTYPE: US!).

Additional collections: MÉXICO. ZACATECAS: 9 mi W of Huajuquilla El Alto, 8.8 mi E of Rio Atengo on sandy tuffs, 17 July 1984, *Michener, Prigge and Meyer* 4465 (A, MEXU, TEX).

Leucophyllum ultramonticola is clearly related to *L. pruinatum* with which it shares the distinctive broadly campanulate corolla tube, leaf shape, vesti-

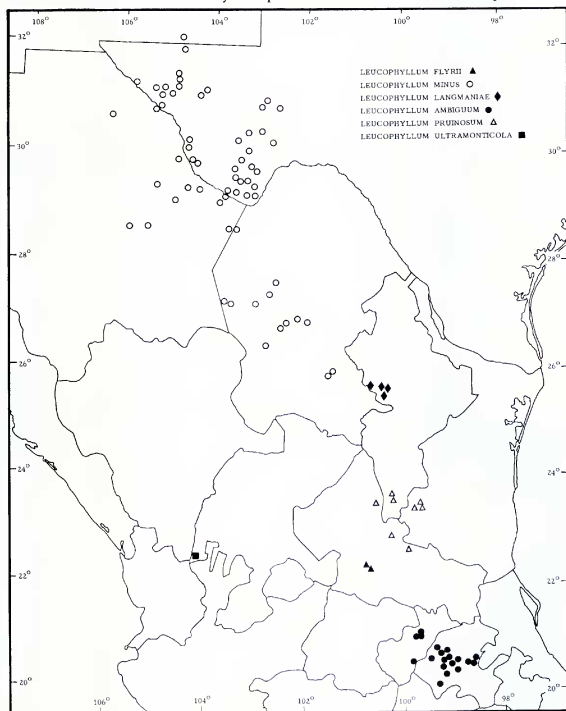


Figure 18. Distribution of *Leucophyllum flyrii*, *L. minus*, *L. langmaniae*, *L. ambiguum*, *L. pruinatum* and *L. ultramonticola* in Trans-Pecos Texas, adjacent New Mexico to Querétaro and Hidalgo in central México.

ture, and texture, and openly branched habit. The new species differs from *L. pruinatum* in its nearly glabrous (not densely pilose) ovary and style base, in its more strongly vestitured (not glabrous) inner lower corolla lobe surfaces, the orange-brown rather than yellow spots on the corolla floor, its slightly larger flowers, generally larger stature with larger, more often orbicular leaves, and its distribution on the Pacific drainage in extreme southwestern Zacatecas (fig. 16). All evidence indicates that it is a rather recent vicariant of *L. pruinatum* of southern Nuevo León, adjacent Tamaulipas, and San Luis Potosí (fig. 18). The new species also shares many characters with *L. ambiguum* of Hidalgo and Querétaro, but the latter has narrower corolla tube-throat, typically lacks yellow-brown spots on the corolla tube floor, and has densely pilose ovary and style bases.

Rose's type specimen collected in 1897, was for a long time the only known collection of *L. ultramonticola*. It has been recently recollected by Michener, Prigge, and Meyer near the type locality where it is locally common on xeric, well-drained, sandy, whitish and reddish volcanic tuffs in association with *Fouquieria splendens*, *Agave*, *Opuntia*, *Jatropha*, *Hyptis*, *Acacia*, *Prosopis* and other leguminaceous shrubs and trees along the road between Huejaquilla El Alto and the Rio Atengo from 1000 to 1500 m elevation just east of San Juan Capistrano in an area that apparently has been very poorly collected.

11. *LEUCOPHYLLUM AMBIGUUM* Bonpl. in Humb. & Bonpl. Pl. Aequinoct. 2:95, pl. 109. 1812. TYPE: MÉXICO. HIDALGO. prope Actopan, 1050 hex., A. Humboldt & A. Bonpland s.n (HOLOTYPE: [Microfiche of Humboldt and Bonpland Herbarium!]).

Leucophyllum campanulatum Miers. Ann. Mag. Nat. Hist. 5:254. 1850. TYPE: *Coulter* 1271 (HOLOTYPE: BM!; ISOTYPES: GH!, K!, NY!, PH!).

Leucophyllum altamiranii Urbina, Anales Inst. Méd.-Nac. México. 8:275. 1906. TYPE: MÉXICO. QUERÉTARO: Del Ciervo al cerro de la Mesa, 20 Aug 1905, *Altamirano* 1557 (HOLOTYPE: unknown).

Strongly, alternately-branched, rounded shrubs 0.6–1.5(-20) dm tall, sometimes somewhat thorny due to persistence of old stems; young stems irregularly, densely gray-tomentose (or brown in herbarium specimens) with cylindric, dendritic trichomes 0.2–0.6 mm long, (0.1-)0.2–0.4 mm in diameter with slender, wavy radii (0.06-)0.1–0.25 mm long, tardily glabrate; old stems light gray to reddish-brown; internodes 1–10(-14) mm long. Leaves alternate, rarely some opposite, sometimes crowded on compressed lateral shoots, broadly ovate to orbicular, rarely broadly elliptical, 8–22(-40) mm long, 5–15(-27) mm wide, often variable on same plant, obtuse-rounded, bluntly apiculate at tip, abruptly cuneate to rounded at base above a broad, 1.5–7 mm long petiole, entire to undulate

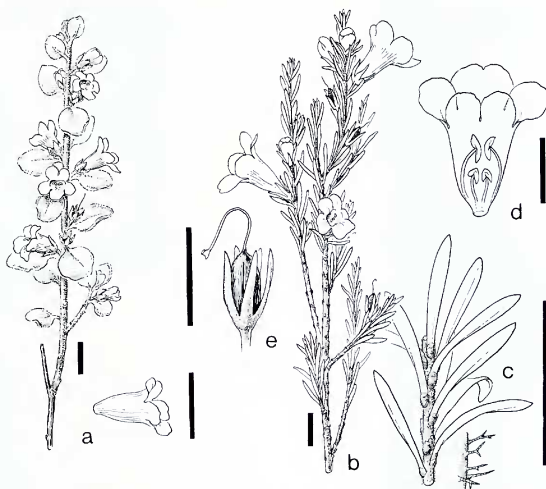


Figure 19. Line drawings of *Leucophyllum pruinosum* and *L. pringlei*. a. *L. pruinosum*. Stem with leaves and flowers. Corolla in side view (lower right) shows characteristic expanded tube (Flyr 564e). b-e. *L. pringlei*. b. Stem with crowded, overlapping leaves and flowers. c. Enlargement of stem and leaves. Note expanded leaf bases and branched trichomes at lower right. d. Transparent view of corolla as seen from above, note relative position of stamens. e. Immature fruit enclosed in persistent calyx and topped with style (R. Cruz C. 2089). Scales = 1 cm.

at margins, densely, irregularly gray (or brownish in herbarium specimens) tomentose on both faces with dendritic trichomes 0.2–0.6 mm long, radii slender, straight or wavy (0.1–)0.2–0.4 mm long, trichomes weathering, becoming more uniform in age, midvein prominent beneath. Flowers with tomentose pedicels 1–2.5(–4) mm long; calyces 4.5–6 mm long, lobes oblong-lanceolate, oblong-ovate, 3–5 mm long, 1–1.5(–1) mm wide, acute, densely tomentose as young stems outside and at inside tip, moderately sericeous-pilose, glandular inside; corollas violet to purple throughout, white only at very base of tube, or with purple spots on floor of tube, rarely white with yellow spots at floor of tube, 12–18 mm long, tube

dorsi-ventrally compressed, three times wider than high, cylindrical to ampliate, lobes obovate to orbicular-reniform, 3–4.5(-6) mm long and wide, undulate, slightly emarginate, ciliate, tube densely pilose throughout inside with long, tangled trichomes to 2 mm long, lobes densely pilose inside with straight trichomes 0.3–0.8 mm long, corolla sparsely stipitate glandular outside; stamens 4(-5), posterior filaments 6–8 mm long, anterior filaments 4–5 mm long, glabrous to pilose; styles 7–13 mm long, pilose; ovaries densely pilose. Capsules 3–4 mm long, densely pilose above, glandular below.

Leucophyllum ambiguum is characterized by its concolorous, broadly ovate, orbicular, petiolate leaves, by its distinctive dendritic trichomes (fig. 20 a) that usually have long, slender, wavy radii 0.2–0.4 mm long on stems and leaves, by its distinctive violet to purple corollas that typically lack a whitish patch on the tube floor, and by the dense tangled and straight trichomes on the inside surfaces of the corolla tube, throat, and lobes. It also is a disjunct species occurring in the southern extension of the Chihuahuan Desert in arid portions of Hidalgo and Querétaro (fig. 18).

Throughout its range it exhibits some notable variation. Occasional plants have shorter vestiture with trichome radii only 0.1 mm long on both stems and leaves. A population northwest of Metzquititlan, Hidalgo, has corollas with a white patch on the floor of the corolla tube beset with yellow spots (*Rzedowski* 32513, ENCB, MEXU; *F. Gonzalez M.* 8486, MEXU) and in this character approaches *L. ultramonticola* and *L. pruinosum*. Occasional plants have some opposite leaves.

Leucophyllum ambiguum occurs on limestone and calcareous hillsides with *Larrea* and other desert shrubs up to submontane scrub from 1200 to 2500 m.

12. *LEUCOPHYLLUM PRINGLEI* (Greenman) Standley, Contr. U.S. Natl. Herb. 23:305. 1923. *Faxonanthus pringlei* Greenman in Sargent, Trees & Shrubs 1:23, pl. 12. 1902. TYPE: MEXICO. PUEBLA: limestone hills near Tehuacan, 6000 ft, 22 Aug 1901, C. G. Pringle 8594 (HOLOTYPE: GH! ISOTYPES: A!, ENCB!, MEXU(2 sheets!), NY!, PH!, US!).

Erect shrubs (1.5-)3–6 dm tall with several erect stems from a thick woody base, irregularly branched above, old branches persistent; young stems terete, 1–1.5 mm in diameter, hispidulous with erect, multicellular, tapering or distally forked or branched, white trichomes 0.1–0.25(-0.4) mm long, and with sessile glands; older stems marked with raised, persistent leaf bases; largest stems 4–6 mm in diameter; bark gray, vertically fissured; internodes 0.5–1(-2.5) mm long. Leaves alternate, crowded in terminal 2–3 cm of branches, linear-lanceolate to linear-

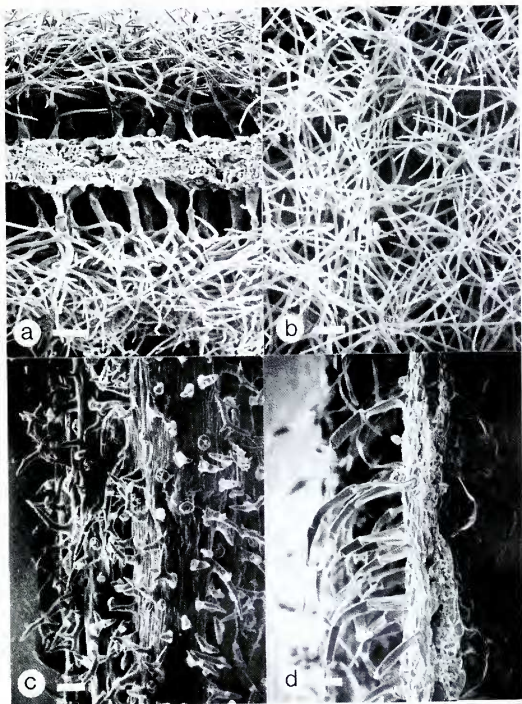


Figure 20. Leaf and stem vestiture of *Leucophyllum ambiguum*, *L. pruinatum*, *L. pringlei* and *Eremogeiton grandiflorus*. a. *L. ambiguum*. Leaf cross section showing equal vestiture on both surfaces and basal simple portion of trichomes. Note also long radii (Flyr 587b). b. *L. pruinatum*. Surface view of adaxial leaf vestiture showing long, slender radii (Henrickson and Heis 19117). c. *L. pringlei*. Vestiture of upper stem with weakly branched trichomes. Note large glands. (Compare with fig. 3 d–f). (R. Cruz C. 2098). d. *Eremogeiton grandiflorus*. Cross section of leaf with adaxial surface on right, abaxial surface with longer unbranched, curved trichomes on left. Note collapsed trichome cells (Stevens, Donoghue, and Scott 2344). Scale in a = 0.1 mm and holds for b–d.

elliptical, 6–12 mm long, 1.2–2.2 mm wide, ca 0.4 mm thick, acute to obtuse at tip, tapering in lower half to a broad petiole-like base about 1 mm long, 0.5–0.7 mm wide but expanded at very base where jointed with stem, entire, typically glabrous except for a few trichomes as in stem on basal 1–4 mm or with trichomes scattered throughout, viscid, strongly glandular to glandular-punctate, midrib obscure. Flowers with ascending pedicels 3–6 mm long with scattered erect to distally forked trichomes, sometimes with short, stipitate glands above; calyces 6.5–8 mm long, tube ampliate, 1–2.2 mm long, lobes 5, linear-oblongate, subequal, 5.5–7(–10) mm long, 0.5–1.5(–2) mm wide, green, leafy, acute at tip, entire, viscid, with sessile (to stipitate) glands on both sides; corollas light purple to blue, with a white patch marked with golded dots on floor of throat, (20)22–25 mm long, tube 1–2 mm long, throat broadly campanulate to 12–15 mm wide (pressed), slightly ventricose at floor, lobes orbicular to obovate, medial anterior lobe largest 9–12(–14) mm long and wide, emarginate, 2 lateral anterior lobes slightly smaller, 8–10 mm wide and long, rounded at tip, posterior lobes 8–9 mm long and wide, rounded at tip, tube with slender, unicellular trichomes 1–3 mm long on floor of distal tube and near throat inside, lobes glabrous inside; corolla glabrous outside; stamens 4, included, posterior filaments 9–10 mm long, anterior filaments 6–7 mm long; anthers whitish, glabrous except for tuft of hairs near tip; proximal anthers 3–3.5 mm long, anterior anthers 2–2.5 mm long; ovaries glandular near tip; styles 10–14 mm long, sparsely glandular to stipitate-glandular, expanded, rhomboid, acute at tip. Capsules 5–6.5 mm long, 2.5–3 mm wide; seeds ellipsoidal, 0.5–0.8 mm long, 0.4–0.5 mm wide, angular, muricate in vertical lines.

Leucophyllum pringlei (figs. 19 b, 20 c) is one of the more distinctive species in the genus and is distinguished by its multicellular, uniseriate, tapering or distally-forked, occasionally distally-branched trichomes with multicellular rays, the tack-shaped, sessile glands with 10–15 cells in the heads (figs. 3 d-f, 20 c), its crowded, linear-oblongate, -elliptical, viscid, glanduliferous, leaves and its habit consisting of a series erect stems developing from a woody knot several centimeters in diameter. Corollas are also broadly ampliate and ventricose along the floor. The stigmas are longer, more rhomboid, acute, and usually recurve at the tip when dried.

In Flyr (1970), the taxon constituted the monotypic genus *Faxonanthus*. However, the species fits well within *Leucophyllum* in flower and fruit characters and differs only in its more open corolla throat (a feature also found in the smaller-flowered *L. pruinosum*), larger-headed glands, trichomes with multicellular rays, and more rhomboid, acute style tips. Its branched or forked trichomes (figs. 3 d, e, 20 c) appear derived from a

broader, dendritic trichome type but with smaller multicellular radii. Equally sparse trichomes also occur in *L. laevigatum* var. *laevigatum*. The conspicuous glands are not unique; leaves of all species of *Leucophyllum* have glands with multicellular heads, those of *L. pringlei* are just larger with a greater number of cells. In other species glands are typically obscured by the crowded, nonglandular trichomes.

Phenetically the taxon is quite distinct and it is here recognized as a separate subgenus. Recognition at the generic level is, in the senior author's opinion, not consistent with other generic distinctions in Scrophulariaceae. The two subgenera share a large number of basic characteristics, particularly those associated with flowers and fruits. Differences lie mostly with vestiture and vegetative morphology. The species is also well-isolated geographically from other species in the genus south of Mexican transvolcanic axis. This isolation has undoubtedly contributed to its morphological distinction.

Leucophyllum pringlei is restricted to limestone slopes in south-central Puebla and adjacent Oaxaca from 1600 to 2350 m (fig. 22) and flowers from May through October depending on rainfall.

11. EREMOGETON Standley & L. O. Williams, *Ceiba* 3:172. 1953. *Gbiesbreghtia* A. Gray, Proc. Amer. Acad. Arts. 8:630. 1873 (non A. Richard & Galeotii 1845). Monotypic.

1. EREMOGETON GRANDIFLORUS (A. Gray) Standley & L. O. Williams, *Ceiba* 3:172. 1953. *Gbiesbreghtia grandiflora* A. Gray, Proc. Amer. Acad. Arts. 8:630. 1873. TYPE: MÉXICO. CHIAPAS: 1864-70, *Gbiesbreght* 723 (HOLOTYPE: GH!).

Large suffrutescent shrubs to small trees 3-6(-8) m tall; young stems subterete, uniformly villous-sericeous to tomentose with mostly soft, antrorsely curved to wavy, multicellular trichomes 0.2-0.7(-1.0) mm long, older stems (3-)4-6 mm in diameter, prominently marked with raised leaf and pedicel bases; bark furrowed; internodes (1-)6-15 mm long. Leaves alternate to subopposite, oblong-obovate, oblong-ovate, elliptical, ovate, (4-)5-9(-12) cm long, (1.5-)2-5(-6) cm wide, obtuse to acute, apiculate at tip, broadly cuneate at base with margins extending down a 8-15 mm long, 2-4 mm wide, winged petiole, at margins coarsely dentate, serrate to crenate in distal part, teeth obtuse to acute, apiculate, revolute, entire and revolute in lower portion, rarely entire throughout, close vestitured on both surfaces, upper (adaxial) surface with more scattered, soft to slightly rigid (then scabrous) tapering, antrorsely curved, multicellular trichomes 0.2-0.5 mm long, often mixed with stipitate glands, lower (abaxial) surface more densely vestitured with similar, tapering, antrorsely curved,

sometimes longer, more wavy trichomes 0.2–0.6(–1.0) mm long, vestiture more tomentose, longer along prominently raised mid and secondary veins. Flowers solitary in leaf axils, pedicels ascending, 2–3.5 cm long at anthesis, to 4–6 cm long in fruit, vestitured as young stems; calyces 5-lobed, lobes green, leafy, oblong, oblong-oblongate, ascending, 2–3.6 cm long, 4–7 mm wide, separate to within 2–3 mm of base, obtuse to acute at tip, entire, vestitured as lower leaf surface outside, with scattered stipitate glands inside; corollas showy, white, turning cream-white or yellowish, opening in late afternoon, zygomorphic, 6–7.2 cm long, tube abruptly expanded above base, cylindrical (25–)35–40 mm long, 15–20 mm in diameter, (25–30 mm wide pressed), posterior 2 lobes united, 25–30 mm long, together 22–28 mm wide, terminal teeth 11–15 mm long, obtuse to acute, erect, anterior 3 lobes spreading to descending, oblong-ovate, 25–33 mm long, 13–15 mm wide, acute to obtuse, corolla thick, glabrous to stipitate-glandular inside, stipitate-glandular outside where exposed in bud, ciliate with longer, crinkled hairs; fertile stamens 2, filaments 55–60 mm long, 1–1.5 mm thick, whitish, glabrous, adnate to expanded corolla tube base; anthers situated near tip of posterior corolla lobes, anther lobes 2, oblong-linear, slightly divaricate, cream-white, glabrous, longitudinally dehiscent across continuous apex, glabrous; sterile stamens 2 or absent, with filaments 3.3–7 mm long; ovary superior glabrous, grooved along septum, 2-loculed, placentae attached medially along septa; ovules many; style accrescent, 6–7.2 mm long, slightly expanded at obtuse tip, stigmatic along broad terminal band, glabrous to sparsely pilose. Fruit of dark brown ovoid, grooved, apiculate capsules, these dehiscent septically to near base, then loculicidally half way to base, subtended by persistent calyx; seeds 50–100 per locule, ellipsoid, 1.7–2.2 mm long, 0.6–0.8 mm wide, dark brown, angulate to flattened by compression, muricate in vertical rows; endosperm oily; embryo small.

Eremogeton (fig. 21) is a very distinct monotypic genus characterized by its uniseriate, multicellular, tapering, unbranched, antrorse trichomes (fig. 20 d), its large, ovate leaves, and its very large flowers with regular, deeply-parted calyces and conspicuous, zygomorphic, thickish corollas, 6–7.2 cm long, with 3 anterior, reflexed to spreading lobes and a 2-toothed, erect, posterior lobe. According to label-data of *W. D. Stevens et al.* 2344, (TEX), the corollas are "white at anthesis, just opening in late afternoon, later cream white." Stamens are typically 2, anterior, however, occasional specimens (including the type) may have two additional abortive, antherless staminodes with short filaments 3–7 mm long (Flyr 1970). The genus also has a conspicuous, probably nectariferous gland on the lower portion of the



Figure 21. Line drawing of *Eremogeton grandiflorus*. Stem with leaves and large flowers; developing fruit with long pedicel at right. (Stevens, Donoghue, and Scott 2344). Scale = 1 cm.

ovary. Capsules are also much larger than in *Leucophyllum* and contain many more seeds.

Eremogeton grandiflorus occurs mostly along limestone bluffs and steep slopes in oak-pine forests of south-central Chiapas, México, and Guatemala from 1200 to 2200 m (fig. 22).

ACKNOWLEDGEMENTS

In January 1970 Lowell David Flyr completed his dissertation in the Department of Botany at The University of Texas at Austin entitled, "A systematic study of the tribe Leucophylleae (Scrophulariaceae)." He recognized 13 species plus two varieties of *Leucophyllum* and the monotypic genera *Faxonanthus* and *Eremogeton*. Unfortunately for the botanical community, Flyr ended his life on 2 November 1971 without publishing his dissertation

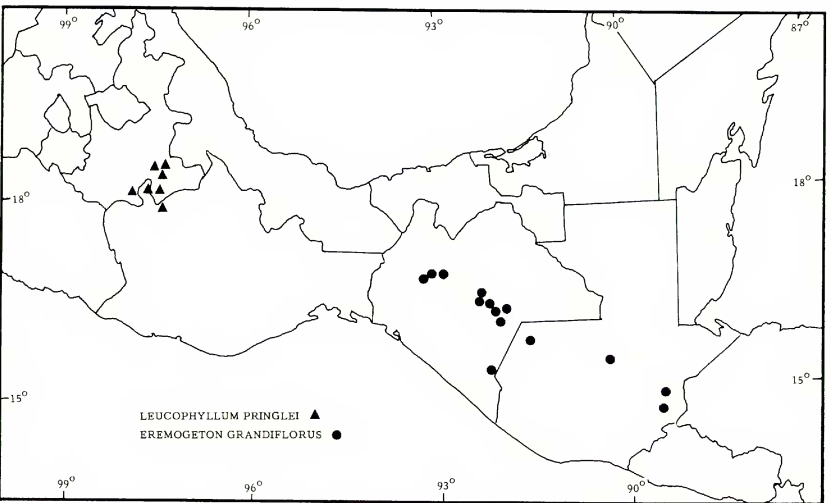


Figure 22. Distribution of *Leucophyllum pringlei* and *Eremogeton grandiflorus* in southern México and Guatemala.

(see obituary by Turner, 1972). In the spring of 1982 Henrickson began a study of the group, using Flyr's dissertation as a starting point, working with the extensive collections at TEX-LL and borrowing or visiting the collections of ASU, ENCB, GH, MEXU, NY, RSA-POM, and US reevaluated the taxonomy and reduced the number of taxa recognized to two genera, *Leucophyllum* (including *Faxonanthus*), with 12 species and 2 varieties, and the monotypic *Eremogeton*. In this treatment the basic systematics of Flyr are followed but descriptions and discussions are largely expanded.

Specimens were visited or borrowed by Flyr from A, BM, CAS, DS, F, GH, K, LA, LL, MICH, MO, MSC, NMC, NY, OXF, PH, SMU, TAES, UC, and US, thanks are extended to curators of these herbaria for loans and courtesies extended. Dr. B. L. Turner, J. Strother, A. M. Powell, R. Irving, J. Rzedowski, P. Echlin, M. C. Johnston, L. H. Shinnars, and others were acknowledged by Flyr (1970) for their help with his dissertation. John Strother, A. S. Tomb, L. Dorr, B. Prigge, D. Michener, J. Mauseth, and K. Nixon as well as B. L. Turner and M. C. Johnston have, in various ways, greatly aided in the preparation of this paper. Robert J. Chinnock of the State Herbarium in Adelaide, South Australia, who is monographing *Eremophila* (Myoporaceae), kindly provided data on characteristics of the Myoporaceae.

REFERENCES

- ARGUE, C. L. 1980. Pollen morphology in the genus *Mimulus* (Scrophulariaceae) and its taxonomic significance. *Amer. J. Bot.* 67:68–87.
- AXELROD, D. I. 1979. Age and origin of Sonoran Desert Vegetation. *Occas. pap. Calif. Acad. Sci.* 132:1–78.
- BARLOW, B. A. 1971. Cytogeography of the genus *Eremophila*. *Austral. J. Bot.* 19:295–310.
- BENTHAM, G. 1846. Scrophulariaceae. in A. P. De Candolle, *Prodromus Systematis Naturalis Regni Vegetabilis* 10:186–598.
- . 1876. Scrophulariaceae. in G. Bentham and J. D. Hooker, *Genera Plantarum* II(2):913–980.
- CARLQUIST, S. 1962. A theory of pedomorphosis in dicotyledonous woods. *Phytomorphology* 11:30–45.
- . 1975. Ecological strategies of xylem evolution. Univ. Calif. Press, Berkeley.
- CRONQUIST, A. 1981. An integrated system of classification of flowering plants. Columbia Univ. Press, New York.
- DE CSERNA, Z. 1960. Orogenesis in time and space in Mexico. *Geol. Rundschau.* 50:595–605.
- DILCHER, D. L. 1974. Approaches to the identification of angiosperm leaf remains. *Bor. Rev. (Lancaster)* 40:1–157.
- FLYR, L. D. 1970. A systematic study of the tribe Leucophylleae (Scrophulariaceae). Ph.D. Dissertation, University of Texas, Austin.
- GUZMAN, E. and Z. DE CSERNA. 1963. Tectonic history of Mexico. *Amer. Assoc. Pet. Geol. Mem.* 2:113–129.

- HAIR, J. B. and E. J. BEUZENBERG. 1959. Contribution to a chromosome atlas of the New Zealand Flora. New Zealand J. Sci. (Wellington) 2:148–156.
- HENRICKSON, J. 1972. A taxonomic revision of the Fouquieriaceae. *Aliso* 7:439–537.
- JOHNSTON, I. M. 1941. New phanerogams from Mexico. *J. Arnold Arbor.* 22:110–124.
- KARRFLAT, E. E. and A. S. TOMB. 1983. Air spaces, secretory cavities, and the relationship between Leucophylleae (Scrophulariaceae) and Myoporaceae. *Syst. Bot.* 8:29–32.
- KIGER, R. W. 1972. A new variety of *Leucophyllum laevigatum* (Scrophulariaceae) from Mexico. *Rhodora* 74:347–349.
- LERSTEN, N. R. and K. A. CARVEY. 1974. Leaf anatomy of Ocotillo (*Fouquieria splendens*; Fouquieriaceae) especially vein endings and associated veinlet elements. *Canad. J. Bot.* 52:2017–2021.
- MICHENER, D. C. 1981. Wood and leaf anatomy of (Scrophulariaceae): Ecological considerations. *Aliso* 10:39–57.
- NIEZGODA, C. J. and A. S. TOMB. 1975. Systematic palynology of tribe Leucophylleae (Scrophulariaceae) and selected Myoporaceae. *Pollen & Spores* 17:495–516.
- RZEDOWSKI, J. 1962. Contribuciones a la fitogeografía florística e histórica de México. 1. Algunas consideraciones acerca del elemento endémico en la flora Mexicana. *Bol. Soc. Bot. México.* 27:52–65.
- . 1973. Geographical relationships of the flora of the Mexican dry regions. pp. 61–72. in A. Graham ed., *Vegetation and vegetational history of northern Latin America*, Elsevier Sci. Publ., Amsterdam.
- STEVENS, P. 1980. Evolutional polarity of character states. *Ann. Rev. Ecol. Syst.* 1:333–358.
- TURNER, B. L. 1972. Lowell David Flyr, 1937–1971. *Sida* 5:54–58.
- VAN DEVENDER, T. R. 1977. Holocene woodlands in the southwestern deserts. *Science* 198:189–192.
- WEBSTER, G. L. 1951. The Polynesian species of *Myoporum*. *Pacific Sci.* 5:52–77.
- WETTSTEIN, R. von. 1891. Scrophulariaceae. In A. Engler and E. K. Prantl, *Die Natürlichen Pflanzenfamilien* 4(3b):39–107.
- . 1895. Myoporaceae. In A. Engler and E. K. Prantl, *Die Natürlichen Pflanzenfamilien* 4(3b):354–360.